



THE UNIVERSITY OF QUEENSLAND  
AUSTRALIA

**Conservation Planning for Primate Communities in Rapidly  
Transforming Landscapes**

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BS in Biology, MS Biological Sciences



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## **Abstract**

Deforestation in tropical forests is a leading cause of biodiversity loss, including for primate species. In this context the processes, habitat loss and fragmentation are two of the main drivers of primate population declines. However, we still know little about the importance of each of these processes (i.e. habitat loss and fragmentation) across different scales for understanding impacts on primate populations. In particular, the vast majority of primate studies on the effect of habitat loss and fragmentation have been conducted only at the patch scale, without paying attention to patterns and processes at broader landscape scales. Understanding how habitat loss and fragmentation affect primate species' occurrence, abundance, group structure is important to propose improved management actions for primates in fragmented landscapes. This thesis evaluates the effect of landscape change on primate species occupancy, abundance, group structure at different scales and incorporates them into a systematic conservation planning process.

The thesis has four aims: 1) determine what we currently know about the effects of patch size in primates and whether or not it varies across life history traits; 2) determine the relative importance of site-scale, patch-scale and landscape-scale variables for primate species occupancy and abundance in the Colombian Llanos; 3) determine the relative importance of site-scale, patch-scale and landscape-scale variables for primate species group density, composition and size in the Colombian Llanos; and 4) based on the model from (3) identify priority conservation areas for primate conservation in the Colombian Llanos, using systematic conservation planning. To address these, I first conducted a systematic review of the published literature to determine what we know about the effects of habitat loss and fragmentation on primate species and whether or not those effects relate to life history traits. Then I use a multi-scale analysis of the variables affecting the occurrence, abundance, group size and composition of primate species in fragmented landscapes, using four primate species of the Colombian Llanos as examples. I then incorporate the models developed for the Colombian Llanos primate species into a prioritization process using systematic conservation planning.

My systematic review shows that density, parasitic prevalence and diversity, and time spent feeding are generally positively correlated with patch size, while species presence and genetic diversity are negatively correlated. Time spent resting and moving did not show clear patterns with changes in patch size. I found little evidence that the effect of patch size varies consistently with traits but this may be due to confounding factors and/or low sample sizes. My novel application of a multi-scaled analysis to primates in the Colombian Llanos demonstrated that occupancy was associated with a combination of patch-site variables, site-landscape or patch-landscape variables depending on the primate species, with site and patch scale variables being the most important in general. Landscape-scale variables were most important at the 1000 m buffer distance (i.e. 1000 m radius distance at which landscape variables were measure from the focal sampling patch) for dusky titi monkeys (*Callicebus ornatus*), black-capped capuchins (*Sapajus apella fatuellus*) and Colombian squirrel monkeys (*Saimiri cassiquiarensis albigena*), and at the 2500 m buffer distance for red howler monkeys (*Alouatta seniculus*). In further examining the effect of these variables on group densities, groups sizes and group composition I show that group densities are primarily associated with landscape variables for most species, while group size is associated primarily by site-scale variables. Group composition for all primate species studied here was largely influenced by group size and therefore, indirectly influenced by site-scale variables. This gives a much more nuanced understanding on how process operating across multiple scales impact on primate populations that can be achieve through the analysis of abundance and occupancy alone. Finally, I apply a multi-scaled approach to conservation planning for primates. The incorporation of combined spatially explicit models and conservation planning tools for primates benefits the prioritising process by considering primate species features such as group size and composition that affects the long-term persistence of these species in fragmented areas. My analysis also leads to an understanding of the role of cost in driving priorities for primate species in fragmented landscapes.

My novel approach to the effects of landscape change on primate species highlights five important contributions for primate conservation. First, I made a quantification of the general effects of patch size on primate species responses finding consistent patterns on primate responses. Second, through this thesis I gained a multi-scaled

understanding of the effect of landscape change on primates. Third, an expansion on the multi-scale approach lead to explicitly link landscape change simultaneously to occupancy, abundance and group structure. Fourth, I include a comparative assessment across multiple species in the same landscape. Finally, this is the first study to apply a multi-scaled approach to conservation planning for primates. My thesis highlight how conservation strategies in fragmented landscapes will affect in different way the group density, size and composition of the primate species studied depending on the scale at which conservation actions are taken. This thesis offers a comprehensive analysis of the importance of landscape approach in primate studies to assess the effects of landscape change at multiple scales.

**Thesis cover photo:** The image shown in the cover is a collage of pictures taken by the candidate in the Colombian Llanos during the fieldwork of this thesis. It represents the rapid landscape changes of the habitat in which these four primate species are living today and which effects are the focus of this work.

## **Declaration by author**

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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## **Publications during candidature**

### **Peer-Reviewed Papers**

**Carretero-Pinzon, X.**, Defler, T.R., McAlpine, C.A., Rhodes J.R. (2015) What do we know about the effect of patch size on primate species across life history traits? Biodiversity and Conservation. The final publication is available at Springer via <http://dx.doi.org/10.1007/s10531-015-1028-z>

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**Carretero-Pinzón, X.** (2013) Population density and hábitat availability of *Callicebus ornatus*, a Colombian endemic titi monkey. In: *Especies de Primates Colombianos en Peligro de Extinción*. Defler, T.R., Stevenson, P.R., Bueno M.L. & D.C. Guzman. Editorial Panamericana, Bogotá, Colombia, pp. 160-169.

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Contributor	Statement of contribution
Xyomara Carretero-Pinzon (Candidate)	Design of research question and data extraction criteria (80 %) Data extraction (100%) Statistical Analysis (70%) Wrote the paper (100%)
Thomas R. Defler	Editorial input and input in Table 2 (25%)
Clive A. McAlpine	Editorial input and input in Table 3 (25%)
Jonathan R Rhodes	Design of research question and data extraction criteria (20 %) Statistical Analysis (30%) Editorial input (50%)

**Contributions by others to the thesis**

No other contributions by other to this thesis that the above mentioned.

**Statement of parts of the thesis submitted to qualify for the award of another degree**

None



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**Keywords**

Habitat loss, fragmentation, primates, Colombia, occupancy, abundance, conservation planning, multi-scale analysis, group size and composition

**Australian and New Zealand Standard Research Classifications (ANZSRC)**

ANZSRC Code	Area of Research	Percent Contributed
050104	Landscape Ecology	50
050202	Conservation and Biodiversity	40
050211	Wildlife and Habitat Management	10

**Fields of Research (FoR) Classification**

FoR Code	Area of Research	Percent Contributed
0501	Ecological Applications	50
0608	Zoology	30
0502	Environmental Science and Management	20

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## List of Abbreviations used in the thesis

AIC Akaike's Information Criteria

FAO Food and Agriculture Organization of the United Nations

GIS Geographical Information System

GPS Global Positioning System

IDEAM Instituto de Hidrología, meteorología y estudios ambientales (Institute of Hydrology, Meteorology and Environmental Studies, acronyms in Spanish).

IUCN International Union for Conservation of Nature and Natural Resources

## Glossary - Definitions

**Akaike's information criteria (AIC):** measure of the estimate of the expected relative distance between the fitted model and the unknown true mechanism that actually generate the observed data (Burnham & Anderson 2002).

**Bayesian state-space model:** hierarchical models that explicitly model the underlying ecological or "state" process fitted within a Bayesian framework (Kéry & Schaub 2011)

**Fragmentation:** refers to the breaking apart of habitat without a loss in the amount of habitat (Fahrig 2003).

**Habitat loss:** reduction in the amount of habitat available in a landscape (Fahrig 2003).

**Planning units:** spatially explicit units in which the priority process is based. Planning units may be defined by overlaying the planning region with a grid of squares or lattice of hexagons. They must capture all the areas that can possibly be selected as part of the reserve system and their size should be at a scale appropriate for both the ecological features you wish to capture and the size of the protected areas likely to be implemented (Game & Grantham 2008).

**Scale:** spatial or temporal dimension of an object or process, characterized by both grain and extent (Weins 1989, Turner et al. 2001). Where grain refers to the finest spatial resolution at which an object or process is observed and the extent refers to the size of the overall study area (Turner et al. 2001).

**Spatial arrangement:** refers to the spatial location of landscape structures (forest patches, crops, water sources) in the space within a defined area.

## **Chapter 1: General Introduction**

Primates are one of the most threatened taxa globally (Rylands et al. 2008a; Schipper et al. 2013; Schwitzer et al. 2015) and their survivorship depends on our understanding of the drivers affecting their persistence at different scales in fragmented areas. Landscape changes produce a reduction in the amount of habitat available to species (habitat loss; Fahrig 2003), and the increases in fragmentation (Fahrig 2003). These influence the population dynamics, extinction risk and other responses of species, through their influence on ecological processes and function (With & King 1999; Fahrig 2002; Pardini et al. 2010; Haddad et al. 2015). The direction of the effects and magnitude of those effects varies with the scale at which habitat loss and fragmentation is studied and the particular species of concern (Turner et al. 2001; Wu & Li 2006). This thesis evaluates the effect of landscape change on primate species occupancy, abundance and group dynamics at different scales and then incorporates this into a systematic conservation planning process.

### **Effects of habitat loss and fragmentation on biodiversity**

It is generally accepted that the effects of habitat loss on biodiversity are strongly negative and outweigh the effects of fragmentation (Fahrig 2003; McAlpine et al. 2006; Villard & Metzger 2014). However, habitat fragmentation also has strong and generally degrading effects on biodiversity and ecological processes (Haddad et al. 2015). In addition, matrix composition (Tscharntke et al. 2012; Villard & Metzger 2014) and edge effects (Laurence et al. 2007) are also important for species persistence in fragmented landscapes. Understanding the effects of habitat loss, fragmentation and composition of the matrix on species is important for conservation biology.

Habitat loss and fragmentation impact not only the presence and abundance of species but also their behaviour (Andrén 1994; Renjifo 2001; King & With 2002; Morante-Filho et al. 2015). Changes in dispersal patterns, feeding behaviours, predation risk and population dynamics have been observed as a consequence of habitat loss and fragmentation in different groups of vertebrates (McIntyre & Wiens 1999; Renjifo 2001; With & King 2002; Anderson et al. 2007a; Boyle & Smith 2010a). For example, changes in group size and behavioural patterns (feeding and/or traveling times) have been observed in primate species living in fragments due to reduction in fragment size (Chapman et al. 2007; Boyle

& Smith 2010a, b). In birds and mammals, predation risk seems to increase with fragmentation and depends on various factors such as distance to the edge, the type of habitat and predator ecology (Irwin et al. 2009; Poulin & Villard 2011). The observed changes due to habitat loss and fragmentation vary depending on their drivers and the scale at which these processes occur.

The drivers of habitat loss and fragmentation depend on the region in which they occur. For example, fire is important for habitat loss in areas of boreal forest, while human population growth and the expansion of productive activities such as agriculture are more important in tropical zones of South America, Africa and Asia (Etter et al. 2008; Hansen et al. 2013). The effects of habitat loss and fragmentation also vary with the magnitude of the drivers and the scale at which those drives occur, which can determine the species extinction thresholds (Andrén 1994; Fahrig 2002; Pardini et al. 2010).

Extinction threshold theory states that there is a minimum amount of habitat for a given species for it to persist in a landscape (With & King 1999; Fahrig 2002; Pardini et al. 2010). This threshold is proposed to occur when less than 30 % of the habitat remains but may vary depending on the species being studied (Andrén 1994; Pardini et al. 2010; Morante-Filho et al. 2015). Although differentiating the effects of habitat loss and fragmentation on species extinction thresholds are difficult due to the general high correlation between fragmentation and habitat loss metrics, habitat loss has been identified as the main factor affecting extinction thresholds (Pardini et al. 2010). Habitat loss is the most important factor because it drives the carrying capacity of habitats and it affect the reproduction rates of species (Pardini et al. 2010).

Habitat loss and fragmentation are processes occurring at the landscape scale, but can vary with the spatial extent and resolution of the landscape (Wiens 1989; Fahrig 2003; Wu & Li 2006). Scale is defined as “spatial or temporal dimension of an object or process, characterized by both grain and extent” (Weins 1989, Turner et al. 2001). Where grain refers to the finest spatial resolution at which an object or process is observed and the extent refers to the size of the overall study area (Turner et al. 2001). In fragmented landscapes, the spatial configuration and composition of the landscape vary with the scale at which these processes are observed and with the scale at which species perceive it (Wiens 1989; Wiens & Milne 1989; Jackson & Fahrig 2012). Scale is referred to as the space and time dimension of the process of study (Wu & Li 2006). In the absence of a priori knowledge of the scale that is important to the species of study, multi-scale analyses

have been used to determine the spatial scale at which management actions need to be taken depending on the species of concern (Martin & Fahrig 2012). For the purpose of this thesis I used a landscape approach in which three scales (site-scale: 1 km transects; patch-scale: 1 – 1080 ha; landscape-scale: 1000 m of buffer distance around forest patches) were used to measure the landscape change effect on primate species.

Studies using a landscape approach allows us to understand how habitat loss and fragmentation influence species population dynamics in terms of the composition and spatial configuration of landscapes and how these elements affect species and ecosystem function (Weins 2002; Fahrig 2003; Fahrig et al. 2011). A strong focus on the scales that are appropriate for the organisms being studied is important to understand the interactions between populations and spatial patterns (Weins & Milne 1989; Turner et al. 2001; Wu & Li 2006) and how these interactions affect species responses. This is particularly true in tropical forests, where the rate of deforestation is one of the main causes of threats for species dependant such as primates.

### **Effects of habitat loss and fragmentation on primates**

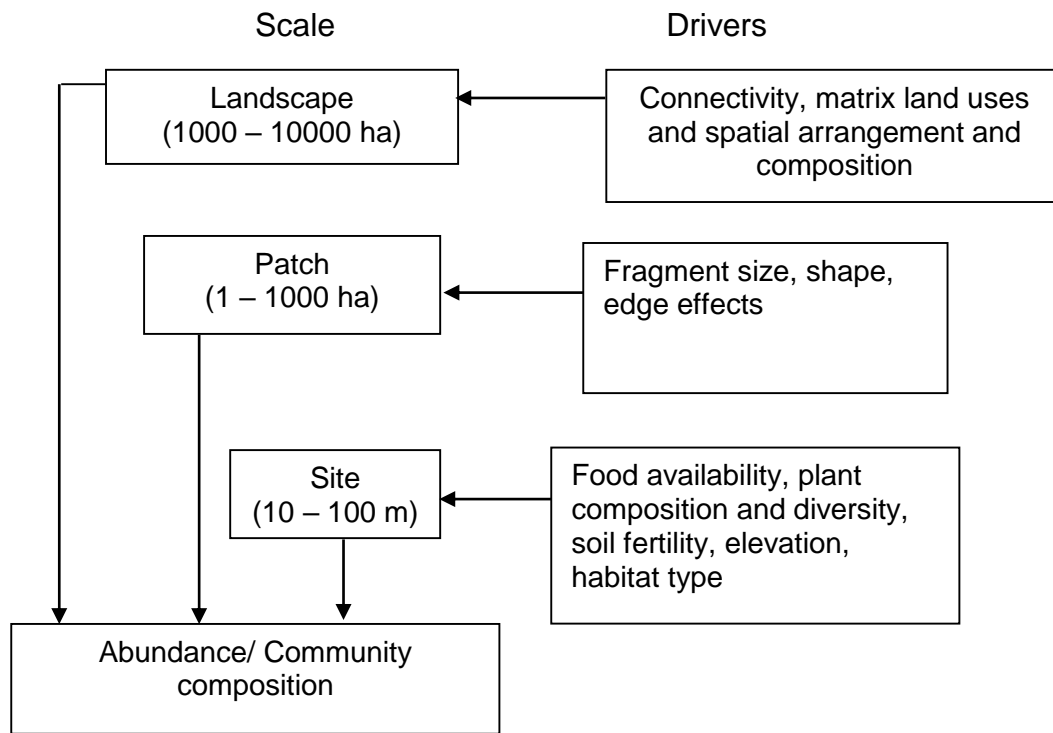
More than 50 % of primate species are threatened globally (Schwitzer et al. 2015). Habitat loss and fragmentation are two of the main drivers of primate species declines (Rylands et al. 2008a; Schwitzer et al. 2015). Although these processes occur at the landscape level, most primate research has been focussed on effects of site and patch scales, with little focus on the landscape scale effects (Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez & Fahrig 2014, Carretero-Pinzón et al. 2015). Therefore, the understanding of the effect of site, patch and landscape variables on primate species' responses to habitat loss and fragmentation is still unclear, but necessary for primate conservation.

Primate studies have followed three different approaches to understand fragmentation and/or habitat loss effects on species responses (Figure 1): (1) studies based on the theory of island biogeography that see primates from a patch perspective, isolated in a hostile matrix, with an emphasis at the site or patch scale; (2) meta-population theory-based studies that include primate movement between fragments in terms of dispersal without an emphasis on the use of the matrix and non-habitat landscape elements; and (3) landscape ecology-based studies which include the landscape scale to understand primate patterns of patch occupation and abundance, including matrix uses (Anzures-Dadda & Manson 2007; Escobedo-Morales & Mandujano 2007; Arroyo-Rodriguez et al. 2008, 2013b; Boyle & Smith 2010b; Pyritz et al. 2010). Most studies have been conducted



using the first approach to assess group changes in ecological and behavioural variables comparing one or several groups in small fragments to one or two groups of primates in a larger fragment or continuous forest (Chapman et al. 2005a; Anderson et al. 2007a; Boyle et al. 2009; Arroyo-Rodriguez & Dias 2010; Abondano & Link 2012). Although we have information on primate species responses to changes in patch size (Carretero-Pinzón et al. 2015), the effect of habitat loss and fragmentation processes at different scale has been done only in a few studies (Thornton et al. 2011; Arroyo-Rodriguez et al. 2013b).

The species-area relationship has been studied globally and for some specific regions for primates, concluding that primate species richness increases with forest patch size, in general (Harcourt & Doherty 2005; Benchimol & Peres 2013). This finding supports one of the predictions of island biogeography theory, that states that bigger fragments have more species compared to smaller fragments (McArthur & Wilson 1967). However, primate studies in fragments have also highlighted the importance of small fragments and the matrix surrounding those fragments for the persistence of primate species in fragmented areas (Anderson et al. 2007b; Chapman et al. 2007; Bicca-Marques et al. 2009; Boyle & Smith 2010b). Most threatened primate species only persist in highly fragmented areas, therefore, understanding the effects of habitat variables at different scales (site, patch and landscape scales, Figure 1), will help us to implement better informed conservation actions for these species.



**Figure 1 Conceptual diagram of drivers affecting primate responses at different scales**

Primate responses to the effects of habitat loss and fragmentation are also highly variable across continents and species (Onderdonk & Chapman 2000; Chapman et al. 2007; Arroyo-Rodriguez & Dias 2010). Changes in behaviour, densities, abundance and presence have been observed that seem to be the product of habitat loss and/or a fragmentation (Chapman et al. 2007; Pozo-Montuy et al. 2008; Arroyo-Rodriguez & Dias 2010). However, we still lack a general analysis of what we know about the effects of habitat loss and fragmentation, basically because of a lack of clear predictors that measure habitat loss and fragmentation separately and at the scale at which they occur (Arroyo-Rodriguez et al. 2013a).

The life history traits of each species also seem to determine primate species responses in some lineages (Alberts & Altmann 2006). But, which life history traits are strong predictors of the effect of habitat loss and fragmentation on primate species are difficult to determine even though they are necessary for designing conservation plans in fragmented landscapes for multiple species. For example, a study of primate responses to habitat fragmentation in fragments outside of Kibale National Park in Africa could not find strong predictors of fragment occupancy for the different primate species studied (Onderdonk & Chapman 2000). This study evaluated primate life history characteristics (home range,

body sizes, group size and degree of frugivory) of six species and patch characteristics (area, distance to the nearest patch, distance to Kibale and number of food trees present) to predict particular primate species presence in forest fragments. No species' life history trait could be identified to explain the observed patterns. In contrast, another field study evaluated primate life history traits (home range site, diet specialization (proportion of fruits in the diet), body size and group size) in six Neotropical primates in the Brazilian Amazon to predict primate species presence. This study found that the proportion of fruit in the diet (a measure of diet specialization) is a good predictor of presence for these primate species followed by home range size (Boyle & Smith 2010b). The contradictory results found in these two studies may be due to small sample sizes, as distribution modelling studies have suggested that at least 100 – 150 sites should be evaluated to predict species distributions, and these authors only evaluated 20 (Morrison et al. 1992). On the other hand, the contradictory findings of these two studies may be related to different evolutionary pressures affecting primate species in Africa and the Neotropics that influence the life history traits of these species (Emmons & Gentry 1983). The role of species traits to predict the effects of habitat loss and fragmentation on primate species needs to be clarified if we want to be able to make generalizations that can inform conservation strategies for primates.

Primate persistence in forest fragments not only depends on fragment size effects but also can be affected by the time that the fragment was formed and other pressures associated with the fragmentation process, such as hunting and edge effects (Wieczkowski 2004; Chapman et al. 2007). There is evidence that some species of old world monkeys (Africa and Asia) have greater resilience to changes produced by human activities. They seem to recover from these disturbances, in terms of population size, after the fragmentation of the habitat. Perhaps the recovery is a compensation effect after other species disappear (McArthur et al. 1972; Peres & Dolman 2000). Another explanation for the resilience of some Old World primates to disturbances may be because they have been in contact with humans much longer (i.e. in terms of evolutionary time) than Neotropical (Central and South America) and Malagasy primates (Madagascar) (Harcourt & Doherty 2005). This pattern of more resilience in African primates has also been observed for other animals and has been used as an explanation for megafaunal extinctions that occurred in Pleistocene/Recent times in other continents and Madagascar (Green et al. 2007). However, threats faced by primates in fragmented landscapes can also be considered at

short scales of time, such as seasonal variabilities in resource abundance that could be due to the product of slight variations in local climate.

Slight variations in climate patterns such as rainfall seems to also affect primate species' responses to habitat loss and fragmentation in fragmented landscapes because of their effects on seasonal fruit production (Chapman et al. 2005b). These changes in fruit production affect primate survivorship and fitness, especially for frugivorous species in smaller fragments and such effects can lead to local extinction of these species (Stevenson & Aldana 2008). Primate species living in fragmented landscapes face additional pressures due to their close proximity to human settlements and to production activities such as agriculture. These pressures can exacerbate the effects of habitat loss and fragmentation on primate species, depending on species' life history traits. For example, the large space requirement of some large bodied primate species living in large groups at times has been overcome by utilising crops and urban resources as part of their diet (Singh et al. 2001; Bicca-Marques et al. 2009; Pozo-Montuy et al. 2012; Campbell-Smith et al. 2012). In addition, some traits such as large body size and diet specialization seem to make species with these traits more sensitive to other concomitant and anthropogenic pressures such as selective logging and hunting (Peres 1999; Chapman et al. 2010). The interaction of these factors in fragmented landscapes has been poorly studied (Michalski & Peres 2005).

### **Conservation planning for primates**

Conservation strategies in primates have focused on the selection of areas to conserve specific primate species or communities, focussing on population and threat analyses (Carlsen et al. 2011; Maldonado et al. 2012; Dunn et al. 2014). However, the rapid deforestation of tropical areas has led to a change in strategy for area selection for primate conservation in recent years, where a landscape perspective and the incorporation of new approaches to conservation planning have begun to be used (Plaza-Pinto & Viveiros-Grelle 2009; Plaza-Pinto & Viveiros-Grelle 2011; Carlsen et al. 2011; IUCN & ICCN 2012; Maldonado et al. 2012). Systematic conservation planning approach and tools have been incorporated only in a few cases (Plaza-Pinto & Viveiros-Grelle 2009; Plaza-Pinto & Viveiros-Grelle 2011; Carlsen et al. 2011). Features of systematic conservation planning such as a transparent process of selection and designing of conservation areas that meet explicit conservation goals at regional or national scales is an attractive approach for

primate species in fragmented areas (Plaza-Pinto & Viveiros-Grelle 2009; Plaza-Pinto & Viveiros-Grelle 2011).

Systematic conservation planning is a structured approach to identifying conservation priorities to meet explicit conservation objectives, in which feedback, revision and reiteration can be incorporated at certain points to re-evaluate the output based on expert knowledge or observed effects of specific management actions (Margules & Pressey 2000; Margules & Sakar 2007; Veloz et al. 2015). Systematic conservation planning includes eight stages: 1) identification and involvement of key stakeholders; 2) goals and objective identification, 3) data compilation; 4) conservation targets and design principles establishment; 5) existing protected areas revision and identification of network gaps; 6) selection of new protected areas; 7) implementation of conservation actions; and 8) maintenance and monitoring of the protected area network (Possingham et al. 2010). One of the central points for the conservation of biological diversity is the establishment of conservation area networks, that are managed for different types of objectives such as minimize the risk of extinction (Margules & Pressey 2000; Margules & Sakar 2007; Pressey et al. 2007). The systematic conservation planning process allows us to prioritise and select some conservation areas over others that perform a conservation function defined by specific goals (Wilson et al. 2006; Peralvo et al. 2007; Veloz et al. 2015). The use of a systematic conservation planning framework implies the use of specific protocols to identify priority areas, explicitly taking into account the cost of implementing conservation actions (e.g. choosing sites to minimizing biodiversity loss given a cost constraint; Wilson et al. 2006; Peralvo et al. 2007).

Systematic conservation planning requires at least six basic concepts that need to be considered in any prioritization process: comprehensiveness, representativeness, adequacy, efficiency, flexibility and irreplaceability (Possingham et al. 2006; Kukkala & Moilanen 2013). The definition of these concepts has varied with time and some of them have been redefined for their use in a spatial prioritization context (Kukkala & Moilanen 2013). One key concept in systematic conservation planning is complementarity, defined as a measure of the contribution an area makes to the full complement of biodiversity features, in a planning region (Margules & Sakar 2007; Ferrier & Wintle 2009; Kukkala & Moilanen 2013). However, it's central role in systematic conservation planning has been debated (Moilanen 2008; Kukkala & Moilanen 2013).

There are two kinds of frameworks used in systematic conservation planning: the area minimization problem and the representation maximization problem (Margules & Sakar 2007). The area minimization problem selects the set of planning units with the minimum total cost in which every surrogate observation feature meets an assigned target (Margules & Sakar 2007; Loyola et al. 2009). The representation maximization problem maximizes the representation of conservation features for a given cost (Margules & Sakar 2007; Illoldi-Rangel et al. 2008).

Systematic conservation planning concepts and methods have been applied to mammals and other vertebrate taxa in Africa (Cowling et al. 2003; Kerley et al. 2003; Brugiére & Kormos 2009), South America (Illoldi-Rangel et al. 2008; Loyola et al. 2009), Madagascar (Kremen et al. 2008) and Asia (Das et al. 2006), including primates, and globally to multiple taxa (Bode et al. 2008). However, only two studies have focused on prioritizing conservation areas for primate species, both with a focus on endemic species of the Brazilian Atlantic forest (Plaza-Pinto & Viveiros-Grelle 2009; Plaza-Pinto & Viveiros-Grelle 2011). In addition, systematic conservation planning tools have been also incorporated in the conservation action plan for specific species such as chimpanzees (Carlsen et al. 2011). Although many primate studies, based on the ecology and behaviour of specific species, have proposed the need to create reserves and conservation actions (Chapman et al. 2007; Chagas & Ferrari 2011; Peng-Fei et al. 2011), none of these have used conservation planning concepts or methods to identify reserves. So, there is a need to incorporate more effective and standardized tools, to select conservation area networks for primates in highly fragmented landscapes. On the other hand, an additional consideration when selecting conservation area networks for primates in highly fragmented landscapes is the presence of regenerating areas. The incorporation of regenerating areas could modify the scale at which management actions need to be taken as well as the areas to protect. Although not used in this thesis, the incorporation of regenerating areas in the systematic conservation planning process has been, for example, applied for two mammal species in the Brazilian Atlantic forest increasing the habitat availability in fragmented landscapes (Crouzeilles et al. 2015).

## **Regional, National and Study Area Context**

The Neotropics is one of the most diverse regions in terms of species richness and endemism (Laurence 2010). Some of the most diverse hotspots are located in South

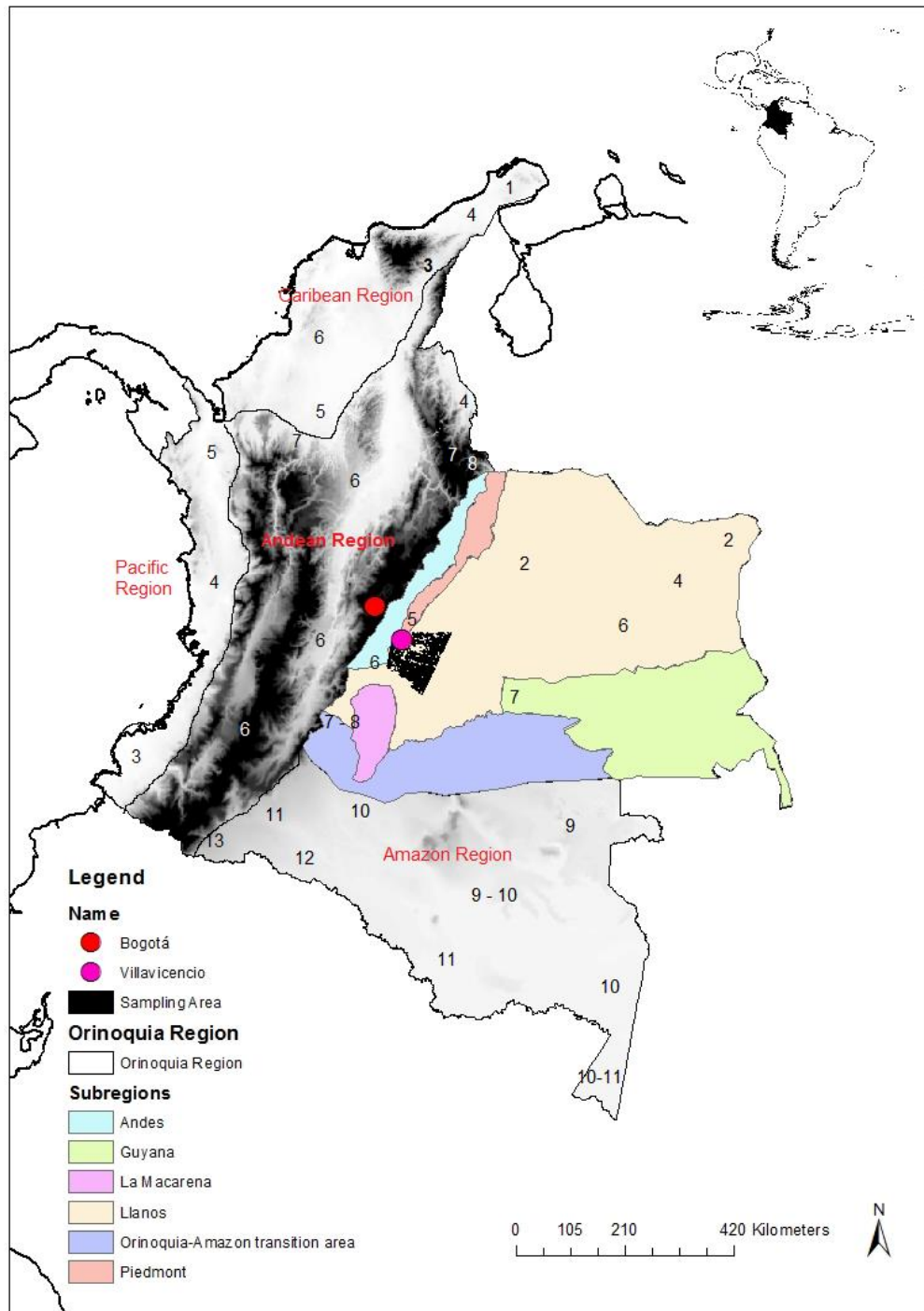
America, such as the Amazon and Atlantic forests (da Silva et al. 2010). Neotropical primates are distributed from southern Mexico to northern Argentina, with the highest levels of primate diversity and endemism concentrated in only three countries: Brazil (131), Peru (51) and Colombia (50) (Mittermier & Oates 1985; Eeley & Lawes 1999; Defler 2010; Solari et al. 2013). The area of greatest primate diversity in Colombia is located in the eastern lowlands of Putumayo department where a species richness (gamma diversity and perhaps alpha diversity) reaches 14 species (Defler 2010). Other primate high diversity areas are found from southern Orinoquia (7-11 species) to many parts of the Colombian Amazon that commonly contained 8-13 sympatric species of primates (Defler 2010, Figure 2).

The Orinoquia region comprises all tributary river and streams of the Orinoco River in Colombia and Venezuela (981.446 km<sup>2</sup>, Lasso et al. 2010). This area is a highly diverse ecosystem, consisting of natural savanna, gallery forest and lowland rain forest. The region is important for fish (658 species, 56 endemics in Colombia), amphibians and reptiles (266 amphibians and 290 reptiles (in Colombia and Venezuela)), birds and 318 species of mammal (most of them in some IUCN category of threat) (Lasso et al. 2010). In, Colombia, the Orinoco region has been a colonization and development frontier since the 16<sup>th</sup> century and it continues to be so today (Stevenson & Aldana 2008). The main drivers of this development frontier is the migration of people from many parts of the country, but also the growth of economic projects due to petrol exploitation, agro-commodities (palm oil plantations that are replacing savanna, pastures and other land uses), livestock (with a long history of land use in this region since the first Jesuit missionaries introduced cattle in the 16<sup>th</sup> century), illegal crops and infrastructure, especially near to the Andes (piedmont, La Macarena and Orinoquia-Amazon transition subregions; Figure 2) (Ecopetrol 2015; Fedepalma 2014; López-Hernandez et al. 2005; Etter et al. 2006a; Carretero-Pinzón & Defler in press). The Orinoco region has a diversity of vegetation covers and geomorphologic formations that were used by Lasso et al. (2010) to define different biogeographic regions (Figure 2). This thesis has focused on the Los Llanos bioregion (Lasso et al. 2010 (light pink area in Figure 2)) and on the black area (Figure 2). It is an area undergoing rapid habitat loss and fragmentation and the prioritization of forest reserves are urgently needed. The study area is located 180 km south of the capital of Colombia, Bogotá and 65 km from the main city of the region, Villavicencio.

Primate diversity in the Colombian Orinoquia, although not comparable in diversity to the Amazon, is high in endemism, especially in the piedmont, La Macarena and Amazon–

Orinoquia transition subregions (Figure 3). There is little information on medium and large mammals in the Orinoquian region, and some primate species do not even have their distribution limits clearly defined (Lasso et al. 2010; Defler 2010; Carretero-Pinzón & Defler in press). However, distribution limits seem to be determined by landscape constraints, such as forest and savannah cover in the Llanos bioregion (light pink area in Figure 2b), compared with a more continuous lowland rain forest towards the Amazon. These vegetation cover changes represent a challenge to primate species due to a reduction of plant diversity which affects resource availability and reduces primate diversity in the Llanos areas of Colombia and Venezuela (Defler 2013). The study area contains five primate species; three of them threatened and endemic (See Table 1 and Appendix A).





**Figure 2. Map of Colombia showing primate species richness in each region of the country (Modified from Defler 2010); and Orinoco Region subdivision (modified from Lasso et al. 2011). Black area highlight the study area selected for this thesis in the Llanos bioregion.**

**Table 1 Primate species present in selected area and their current threat status using IUCN criteria (National and International threat status).**

Family	Species	Common Names	International Threat Status	National Threat Status
Aotidae	<i>Aotus brumbacki</i>	Brumback's night monkey	Vulnerable*	Vulnerable**
Atelidae	<i>Alouatta seniculus</i>	Red howler monkey	Least Concern**	Least Concern**
Cebidae	<i>Saimiri cassiquiarensis</i>	Colombian squirrel monkey	Near Threatened††	Vulnerable†
	<i>albigena</i> <sup>1</sup> (= <i>Saimiri sciureus albigena</i> ) <sup>1</sup>			
	<i>Sapajus apella</i>	Black-capped capuchin	Least Concern†††	Least Concern**
Pitheciidae	<i>fatuellus</i> <sup>2</sup> (= <i>Cebus apella</i> )			
	<i>Callicebus ornatus</i>	Dusty titi monkey	Vulnerable****	Vulnerable**

\* Morales-Jiménez et al. 2008; \*\* Defler 2010; †Carretero-Pinzon et al. 2009; ††Boubli et al. 2008b; †††Rylands et al. 2008b

<sup>1</sup>Taxonomy according to Mittermeier et al. 2013.

<sup>2</sup>Taxonomy according to Ruiz-Garcia & Castillo, in press.

## Aims and Objectives

This thesis evaluates the effect of landscape change on primate species occupancy, abundance, group size and composition at different scales and incorporates them into a systematic conservation planning process. This thesis has four aims: 1) determine what is currently know about the effects of patch size in primates and whether or not it varies across life history traits; 2) determine the relative importance of site-scale, patch-scale and landscape-scale variables for primate species occupancy and abundance in the Colombian Llanos; 3) determine the relative importance of site-scale, patch-scale and landscape-scale variables for primate species group density, composition and size in Colombian Llanos; and 4) based on the model from (3) identify priority conservation areas for primate conservation in the Colombian Llanos, using systematic conservation planning (Figure 3).

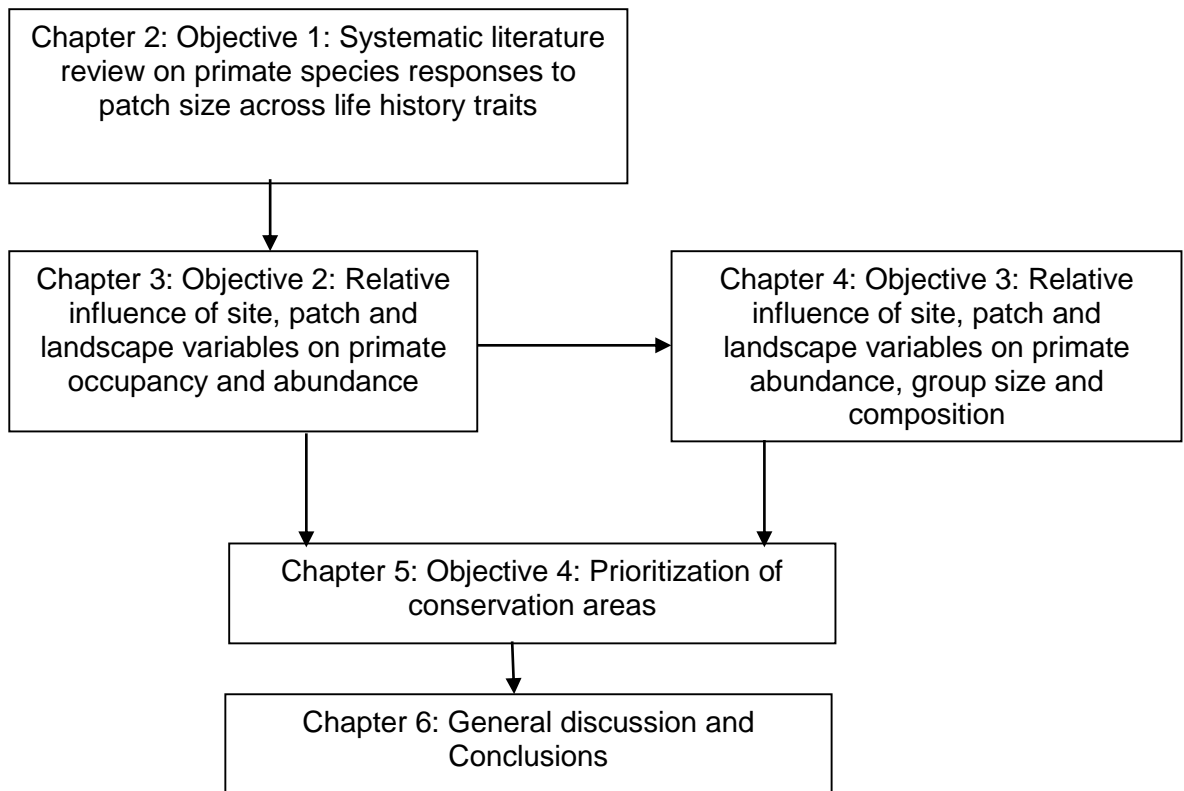
To accomplish this, first I did a meta-analysis (Chapter 2) using a systematic review to determine what we currently know about the effect of patch size on primates by answering the following questions: 1) what are the general responses of primates to patch size across a range of response variables? (2) how much variation is there in the responses of different primate species to patch size? and (3) are there any consistent relationships between traits and primate species' responses to patch size? To address these questions, I conducted a review of published literature on the effects of habitat loss and fragmentation to quantify the effect of these processes on primates and whether these effects depend on species' traits. The effect of patch size on seven response variables (density, parasite prevalence and diversity, presence, genetic diversity, time spent feeding, resting and movement), was extracted from 135 papers and these were compared across six species traits (diet specialization, social structure, body size, home range size, group size and dispersal ability). I found that density, parasitic prevalence and diversity, and time spent feeding were positively correlated with the combined effects of patch size, while species presence and genetic diversity were negatively correlated. Time spent resting and moving did not show clear patterns. I found little evidence that the effect of patch size varies consistently with traits but this may be due to confounding factors and/or low sample sizes.

Then, I present the results of a multi-scale analysis on the effects of habitat loss and fragmentation on primate occupancy and abundance for four diurnal species in the Colombian Llanos (Chapter 3). I quantify how important landscape-scale forest area and configuration are relative to patch-scale and site-scale habitat variables for the occupancy and abundance of four primate species in the Colombian Llanos. I collected presence and abundance data from 81 fragments stratified by fragment size and the proportion of forest surrounding each forest fragment, for four primate species (red howler monkeys (*A. seniculus*), black-capped capuchins (*S.a. fatuellus*), Colombian squirrel monkeys (*S.c. albigena*) and dusky titi monkeys (*C. ornatus*)). I found that occupancy was determined by a combination of patch-site variables, site-landscape or patch-landscape variables depending on the primate species, with site and patch variables being more important. The best models contain variables at the site, patch and the 1000 m landscape spatial extent variables for two of the four studied species (black-capped capuchins (*S.a. fatuellus*) and Colombian squirrel monkeys (*S.c. albigena*)) and the 2500m landscape spatial extent variables for red howler monkeys (*A. seniculus*). For dusky titi monkeys (*C. ornatus*) the best model contained site variables and 1000m landscape spatial extent variables.

In addition, I present the results of a multi-scale analysis on the effects of habitat loss and fragmentation on primate species group composition and size for four diurnal species in Colombian Llanos, in Chapter 4. I used a hierarchical model to assess the effect of habitat loss and fragmentation on the number of groups, the group size and the composition for four primate species in the Colombian Llanos. I found that group densities are primarily driven by landscape variables for most species, while group size is influenced primarily by site-scale variables. Group composition for all primate species studied here was largely influenced by group size and therefore, indirectly influenced by site-scale variables. Therefore, conservation strategies in fragmented landscapes will affect in different way the group density, size and composition of the primate species studied depending on the scale at which the conservation actions are taken.

Finally, in Chapter 5, I present the results of a conservation planning analysis to determine priority conservation areas for four diurnal primate species in the Colombian Orinoquian subregion of Los Llanos. I used a systematic conservation planning approach and Marxan software to evaluate the spatial arrangement and the most cost-efficient solution to prioritize conservation areas for primates in a highly fragmented landscape, using three different cost (patch area, distance to nearest town and the combination of area and distance to nearest town). I found that although the shape of the relationship between cost and targets is similar for the costs analysed (i.e. area, inverse distance to nearest town and the combination of both), the conservation target was achieved at a lower relative cost by using the combination cost compared with areas and inverse distances to the nearest towns. In addition, each cost structure showed a different spatial arrangement indicating the sensitivity of conservation priority to cost assumptions. For the study region considered here, the north-east and south-east parts of the study region, that concentrate a good proportion of the selected fragments, seems to be the zones in which primate conservation need to focus.

In Chapter 6 I present a discussion of the findings of this thesis and present the main conclusions. This thesis highlights the importance of multiscale studies in which clear predictors at each scale (site, patch and landscape) are defined and how the management and conservation actions that are developed can affect in different ways the population dynamics of primate species, depending on the scale at which those actions are taken and the species of study. Additionally, I present a transparent and replicable approach to selected conservation areas for primates in a highly fragmented area.



**Figure 3. Diagram of thesis structure.**

## **Chapter 2: What do we know about the effect of patch size on primate species across life history traits?**

(Published in Biodiversity and Conservation)

### **Introduction**

Habitat loss and fragmentation are among the primary causes of biodiversity loss worldwide (McGarigal & Cushman 2002; Hanski 2011). Habitat loss is defined as a reduction in the amount of habitat available for a species (Fahrig 2003; Ewers & Didham 2006). On the other hand, fragmentation per se is defined as the breaking apart of habitat (Fahrig 2003). Because landscape change tends to influence both the amount of habitat and the level of fragmentation the effect of these two processes on species needs to be understood to develop effective conservations plans. Empirical evidence suggests that habitat loss tends to have negative effects and outweighs the more variable effect of fragmentation (Fahrig 2003; McAlpine et al. 2006; Villard & Metzger 2014). However, recent studies also highlight the importance of the composition of the habitat, matrix (Dunning et al. 1992, Tscharntke et al. 2012, Villard & Metzger 2014), and edge effects (Laurence et al. 2007) on biodiversity loss. These effects may therefore complicate the interpretation of the effect of habitat loss and fragmentation on biodiversity. Nonetheless, seeking generalities about the effects of habitat loss and fragmentation is desirable as a means of informing conservation decision-making.

Primates are among the world's most threatened taxa (Mittermeier & Oates 1985; Rylands et al. 2008a; Schipper et al. 2008) and they commonly occur in landscapes subjected to high levels of habitat modification (Schipper et al. 2008; Marsh et al. 2013). However, currently there is a lack of general insights into the effect of habitat loss and fragmentation for primates and whether their effects vary across primate species (Boyle & Smith 2010b; Vetter et al. 2011; Arroyo-Rodriguez et al. 2013a, Arroyo-Rodriguez & Fahrig 2014). Understanding whether any generalities can be made about responses of primates to habitat loss and fragmentation is important because species vary markedly in their life history characteristics and the types of habitats that they occupy (Onderdonk & Chapman 2000; Gibbons & Harcourt 2009; Defler 2010; Mittermeier et al. 2013). Therefore, the responses to habitat loss and fragmentation may also vary from species to species and/or among habitats (Bicca-Marques 2003; Chapman et al. 2006a, 2007; Anderson et al.

2007a, 2007b; Bicca-Marques et al. 2009; Boyle & Smith 2010b; Arroyo-Rodriguez et al. 2013b).

The vast majority of studies evaluating the effect of habitat loss and/or fragmentation on primate species have focussed on the effects of patch or fragment size and isolation (Harcourt & Doherty 2005; Arroyo-Rodriguez et al. 2013a; Arroyo-Rodriguez & Fahrig 2014; Benchimol & Peres 2013). Patch size is a measure that implies both habitat loss and fragmentation, although without making a distinction between them (Fahrig 2003). Isolation, generally measured as distance to the nearest fragment, is a predictor of habitat loss (Fahrig 2003). Although primate studies about the effect of habitat loss and fragmentation are primarily undertaken at the patch scale rather than the landscape scale (Arroyo-Rodriguez et al. 2013a), they provide some insights into the effects of patch size across different primate response variables. For example, a reduction of fragment size seems to decrease the probability of occurrence of primate species, especially those with habitat and diet restrictions (Harcourt & Doherty 2005; Chapman et al. 2006a; Benchimol & Peres 2013). On the other hand, the abundance of primate species seems to be highly variable in response to fragment size depending on habitat features such as food availability (Chapman et al. 2006b; Baranga et al. 2013). Some authors have found higher densities in small fragments compared to large, while other authors have found the opposite (Golçalves et al. 2003; Wieczkowski 2004; Wagner et al. 2009; Carretero-Pinzón 2013a). In addition, an increasing prevalence of parasites and parasitic diversity has been associated with primates living in fragments when compared to those living in continuous forest (Gillespie & Chapman 2008; Mbora & McPeck 2009; Mbora et al. 2009). Reviews and meta-analyses have successfully been used to elucidate trends in primate behavioural flexibility (Gonzalez-Zamora et al. 2011), to determine variation in and how much knowledge about primate responses to habitat fragmentation exist (Bicca-Marques 2003; Arroyo-Rodriguez & Dias 2010), and to clarify trends in species-area relationships (Harcourt & Doherty 2005; Gibbons & Harcourt 2009; Benchimol & Peres 2013). However, there is a need for a more general synthesis of the effects of patch size and isolation across primate species traits in order to derive general insights and to suggest broader statements about the effects of these two measures of habitat loss and fragmentation.

A complicating factor is that species can respond quite differently to habitat loss and/or fragmentation due to differences in life history and behavioural characteristics (Henle et al. 2004; Ewers & Didham 2006). For example, body size can explain large mammal susceptibility to local extinctions due to habitat loss and fragmentation processes

(Thornton et al. 2011). Similarly, species with high flexibility in behavioural responses, such as diet and habitat, tend to be more tolerant of habitat loss and fragmentation effects, such as in birds (Renjifo 2001; Vetter et al. 2011; Newbold et al. 2012) and mammals (Hockey & Curtis 2008; Thornton et al. 2011). Traits associated with dispersal capacity, niche breadth and reproductive rate have also been found to determine butterfly and moth species' responses to habitat loss and fragmentation (Öckinger et al. 2010). In mammals, diet specialisation makes some groups, such as nectarivores and herbivores, as well as species able to use open areas, less susceptible to the negative effects of forest fragmentation (Vetter et al. 2011). This variation in the response of species to habitat loss and fragmentation is an important driver of conservation priorities (Henle et al. 2004; Thornton et al. 2011; Vetter et al. 2011).

In primates, life history traits and sensitivity to environmental changes, such as landscape change, have been found to be related (Irwin 2008; Boyle & Smith 2010b). This may be particularly true for traits such as body size, diet specialisation, home range size, habitat requirements, and the ability to traverse the matrix (Antongiovanni & Metzger 2005; Chapman et al. 2006a; Anderson et al. 2007a, 2007b; Boyle & Smith 2010b). Many of these traits have been suggested as important variables determining the presence of primate species in habitat patches in fragmented landscapes (Boyle & Smith 2010b). However, few studies have attempted to specifically quantify variation in responses among different species with different traits to understand primate responses to habitat loss and/or fragmentation (but see Onderdonk & Chapman 2000; Chapman et al. 2006a; Boyle & Smith 2010b). It is unclear if there is any generality in trait effects. No previous reviews have attempted to evaluate the variation in responses to patch size across primate species traits, for all primate species using published literature.

The aim of this paper is to use a systematic review to better understand the effect of patch size as measures of habitat loss and fragmentation on primates by answering the following questions: 1) what are the general responses of primates to patch size across a range of response variables? 2) how much variation is there in the responses of different primate species to patch size? and 3) are there any consistent relationships between traits and primate species' responses to patch size?



## **Methods**

### **Hypothesis**

First I developed a conceptual framework for the hypothesised influence of decrease in patch size on primate species as a function of their traits across a number of response variables. Patch size impacts primate species as a consequence of the loss and isolation of habitat and other processes associated with anthropogenic habitat degradation (Benchimol & Peres 2013). These other processes include shortages of resources due to selective logging or the extraction of natural resources used by humans, and to higher rates of hunting and persecution for the pet and biomedical markets (Mittermeier et al. 2006; Marsh et al. 2013). However, species responses to patch size are expected to vary due to differences in their life-history traits (Henle et al. 2004; Ewers & Didham 2006; Öckinger et al. 2010).

In developing this conceptual framework, I focussed on a limited number of life history traits and response variables that have previously been proposed as important. The response variables I considered were presence, density, parasitic prevalence and diversity, genetic diversity and behaviour (time spent on resting, feeding and moving). The traits I considered were body size (Ewers & Didham 2006; Stevenson & Aldana 2008; Boyle & Smith 2010b), diet specialisation (Johns & Skorupa 1987; Chapman et al. 2006a; Boyle & Smith 2010a, 2010b), home range size (Skorupa 1986; Dale et al. 1994; Gascon & Lovejoy 1998; Boyle & Smith 2010a, 2010b), group size (Irwin 2007; Boyle & Smith 2010a, 2010b), dispersal ability (Anderson et al. 2007b), and social structure (Chapman & Rothman 2009). Detailed definitions of the category traits used in this review are in Table 2.

**Table 2 Species traits categories and definitions used in this study.**

Species Trait	Category Name	Category Description
Diet Specialization	Frugivorous	More than 80% of diet is composed of fruits. For this study, we also included here primate species categorised as seed predators
	Folivorous	Primate species that mainly consume leaves and vegetative parts
	Omnivorous	Primate species that consume a variety of food items, including insects, vertebrates, fruits and flowers
	Gumivorous	Primate species specialised to consume gum
Social Structure	Multi-male, multi-female and fission-fusion	Groups composed of several males and females, all reproductively active. This category includes groups able to divide into small parties (fission-fusion) to develop daily activities and usually grouping together for the night resting
	One male	Group composed of one male and several females
	Family groups / Noyau	Groups composed of a pair (adult male and female) and their offspring / Social structure in which an individual male have a large home range which include the home range of several females and their immatures
	Polyandrous	Groups composed of an adult female and two males, in which both males mate and help to rear the offspring
Body Size	Large	Primate species of more than 10 kg
	Medium	Primate species between 2 and 10 kg
	Small	Primate species of less than 2 kg
Home Range Size	Large	More than 50 ha
	Small	Less than or equal to 50 ha
Group Size	Large	More than 10 individuals
	Small	One to nine individuals
Dispersal Ability	Arboreal	Primate species strictly arboreal, which in continuous forest never goes to the ground.
	Terrestrial	Primate species mainly terrestrial, which develops most of their daily activity on the ground
	Both	Primate species which develop daily activities on the ground as well as in the trees.

I then developed a series of hypotheses about the effect of a decrease in patch size on each response variable and how each trait influences these responses. Overall I hypothesised that a decrease in patch size would increase density, parasitic prevalence and diversity, and time spent moving and feeding, and decrease presence, genetic diversity and time spent resting (Table 2). We also hypothesised that the magnitude of the responses would depend on species' traits and therefore I developed specific predictions about how each trait influences the size of the responses to patch size (Table 3). Few studies explicitly distinguished the effect of habitat loss from fragmentation, by using landscape variables and not only patch size and isolation, so I did not attempt to differentiate the effect of these two different processes (see Anzures-Dadda & Mason 2007; Escobedo-Morales & Mandujano 2007; Arroyo-Rodriguez et al. 2008; Pyritz et al. 2010; Arroyo-Rodriguez et al. 2013b).

## **Review**

A literature search for primate studies was conducted using two general databases (Web of Science and Proquest (research library)) and a specific primate database (PrimateLit at Wisconsin University, USA). This search included papers and books published from 1900 until December 2013. Articles in English, Spanish, Portuguese and French were included in this search. The search for published articles was conducted using a combination of the following key words: "fragmentation", "primates", "primate communities" and "habitat loss". An additional search in Google Scholar for papers in Spanish, Portuguese and French was then conducted using the same key words.

**Table 3 Rationale of *a priori* predictions formulated for effects of a decrease in patch size on the response variables across species traits. A plus (+) represents an increase in the response variable, while a minus (-) represents a decrease in the response. The number of plus and minus represents the magnitude of the expected effect across traits.**

Trait Rationale	Category Trait	Response						
		Density	Parasitic prevalence and diversity	Presence	Genetic diversity	Time spent feeding	Time spent resting	Time spent moving
<b>Dispersal Ability:</b> The dispersal ability of primate species between fragments seems to be determined by their ability to move on the ground (1, 2, 3, 4) and matrix composition (5, 3, 6, 7).	Ground movement	++	++	--	--	+++	--	+++
	Strictly arboreal	+++	+++	-	-	++	-	++
<b>Body Size:</b> Body size has been proposed as a determinant of primate species presence and persistence in fragmented habitats (7, 8, 9). Large body-sized primates, are more sensitive to habitat loss and fragmentation due to their wide-ranging patterns of space use and large amounts of resources needed to supply their basic needs (10).	Large	++	+	--	--	+++	--	++
	Medium	++	+	-	--	+++	--	++
	Small	+++	+	-	--	+++	--	++
<b>Diet Specialisation:</b> The degree of frugivory or specialisation in diet has been proposed as a characteristic that makes	Folivorous	+++	++	-	--	+++	--	++

<p>primates more sensitive to habitat loss and fragmentation (7, 11, 12). These two processes are associated with a reduction in resource availability and changes in plant diversity and abundance, leading to changes in diet composition and high dietary flexibility (13, 14, 15, 16). Restrictions in diet are reflected in the activity patterns, time spent moving, feeding, resting and in social activities (15). Food resources determine the time and distance needed to search and obtain those resources, with fruits requiring more time, and in some cases longer travel distances, to obtain (17).</p>	Frugivorous	++	+++	- -	- -	+++	-	+++
	Omnivorous	++	++	-	- -	+++	-	++
	Gumivorous	++	+++	- -	- -	+++	-	+++
<p><b>Home Range Size:</b> Wide-ranging species that require large home range areas to persist have been proposed as more sensitive to habitat loss and fragmentation than species with small home range sizes (7, 10).</p>	Large	++	+	- -	-	++	-	++
	Small	+++	+	-	-	++	- -	++
<p><b>Group Size:</b> Living in a group puts constraints on species' behaviour and access to food resources (17), increasing daily movement distances and time traveling (15, 18, 19, 20). Although some species are able to live in smaller group sizes, this reduction puts additional constraints on resource defense and</p>	Large	++	+++	- -	- -	+++	-	+++
	Small	+++	++	-	-	++	- -	++

reproductive opportunities that can lead to local extinction (21). Presence of species which are living in small groups may be at higher densities as a consequence of the loss of species that live in large groups (density compensation effect; 22).								
<b>Social structure:</b> Changes in social structure, due to limited opportunities to disperse and a reduction in food resources, have been observed as a consequence of habitat loss and fragmentation (21, 23). However, which types of social structure are most susceptible to habitat loss and fragmentation is not clear. Social structure types include: multimale – multifemale groups, fission-fusion, one male or age-graded group, polyandrous and solitary, noyau and family groups (24).	♀♀♂♂/ Fission-Fusion	+++	+	- -	- -	+++	-	++
	One male	++	+	- -	- -	+++	-	++
	Family groups/ Noyau <sup>a</sup>	++	+	- -	- -	+++	-	++
	Polyandrous	++	+	- -	- -	+++	-	++

<sup>a</sup>Noyau: social structure in which an individual male has a large home ranges, which include the home range of several females and their immature (Fleagle 1999).

1. Naughton-Treves 1998; 2. Cowlshaw & Dunbar 2000; 3. Anderson et al. 2007b; 4. Oliveira et al. 2011, 5. Ehardt et al. 2005; 6. Asencio et al. 2007; 7. Boyle & Smith 2010a; 8. Ewers & Didham 2006; 9. Stevenson & Aldana 2008; 10. Thornton et al. 2011; 11. Skorupa 1986; 12. Johns & Skorupa 1987; 13. Estrada & Coates-Estrada 1988; 14. Chapman & Chapman 1990; 15. Gonzalez-Zamora et al. 2011; 16. Boyle et al. 2012; 17. Peres & Janson 1999; 18. Milton 1980; 19. Chapman 1990; 20. Wrangham et al. 1993; 21. Boyle & Smith 2010b; 22. McArthur et al. 1972; 23. Irwin 2007; 24. Fleagle 1999.

In the first phase, a selection of papers based on the title and abstract was conducted to identify articles that studied primate species or communities in habitat fragments. I included peer-reviewed articles and book chapters, but review articles and meeting abstracts were not included. Review articles were, however, used to detect key references not detected in the database search. Other papers excluded from this systematic review were papers without information on habitat loss and fragmentation, theoretical papers, and papers evaluating effects of logging inside National Parks, hunting, and disturbances not related to habitat loss and fragmentation due to human activities, such as hurricanes. The variety of uses of the term “habitat” in the studies included is a limitation when comparing studies in different habitats. I therefore only included papers on primate species that inhabit forest habitats such as rainforest, dry forest, swamp forest, temperate forest, and spiny forest. I did not include papers relating to primate species living in non-forest habitats, except the ones living in forest remnants within agricultural and urban landscapes. I found 275 articles that met these criteria.

The second phase consisted of a more detailed revision of the selected articles, in order to extract information about the primate species’ traits and the effect of patch size on primates. Only papers where the effect of patch size on presence, density, parasitic prevalence and diversity, genetic diversity or behaviour were stated or could be inferred from the results and discussion were included. These papers address one or several of the response variables chosen for this review. The papers selected had information about fragment size (i.e., they stated the size of all fragments studied or the range of fragment sizes studied) and they were studies that included repetitive sampling of the same fragments through time, or studies that involved primate groups followed for more than six months. Some papers covering studies of shorter duration were included if they contained detailed information on primate densities at several points in time or evaluated the presence of primate species in a high number of fragments, showing trends for some species (i.e., more than 20 fragments). The criteria in this second phase were met by 135 publications (Appendix B).

I evaluated the response variables to habitat loss as changes in the response due to patch size only, because this is the predictor most used in the selected primate literature, independent of the type of design or methodology used to analyse the data, and gives us a mechanism to compare different studies (Appendix B). From each study I recorded

information on the effect of patch size as: 1) positive, if an increase in the response variable studied was reported with decrease in patch size; 2) negative, if a decrease in the response variable was reported with decrease in patch size; or 3) none, if no change in the response variable was reported with decrease in patch size. None of the articles looked at primate species traits per se. I then identified the traits of the species studied using alternative literature (Mittermeier et al. 2013). For each species, data for the following traits were extracted: body size, diet specialisation, home range size, group size, dispersal ability and social structure (see Table 2 for categories and definitions of trait categories used).

## **Analysis**

All papers included in this review used patch size as one or the only predictor to measure habitat loss and fragmentation effects on primate species. Some of the papers also included other variables at patch and landscape scale (only seven papers include landscape variables). However, the only consistent predictor across all papers included was patch size. I therefore used patch size as my predictor to compare the effect of habitat loss and fragmentation across traits and to test my predictions. For each response variable I counted the number of studies that recorded negative, positive or no response to patch size reduction. For each response variable I used  $\chi^2$  tests (Zar 1996) to test whether the frequency of negative, positive and no response was significantly different from random. For each response variable/trait combination I then constructed contingency tables of the number of studies finding different effects (positive, negative or no response) for each trait value. For each of these response variable/ trait combinations I tested for an association between the effect (positive, negative and no response) and trait values using  $\chi^2$  tests (Zar 1996). We used STATGRAPHICS PLUS 2.0 for the statistical analysis.

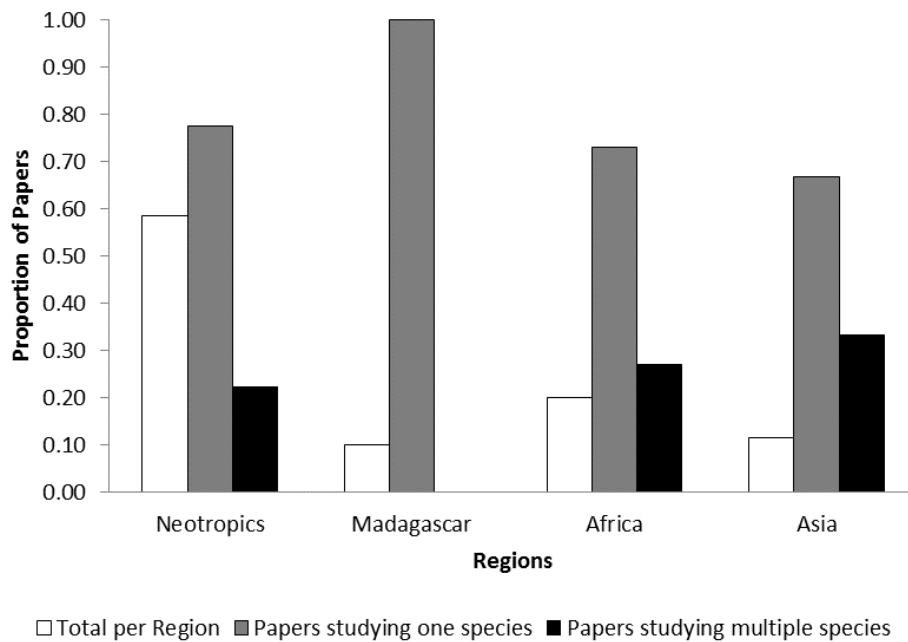
## **Results**

### **Primate studies and species across continents**

The vast majority of studies that quantify density, presence, parasitic prevalence and diversity, genetic diversity and behavioural responses to patch size have been conducted in the Neotropics, followed by Africa, Asia and Madagascar (Figure 4). Most studies focus



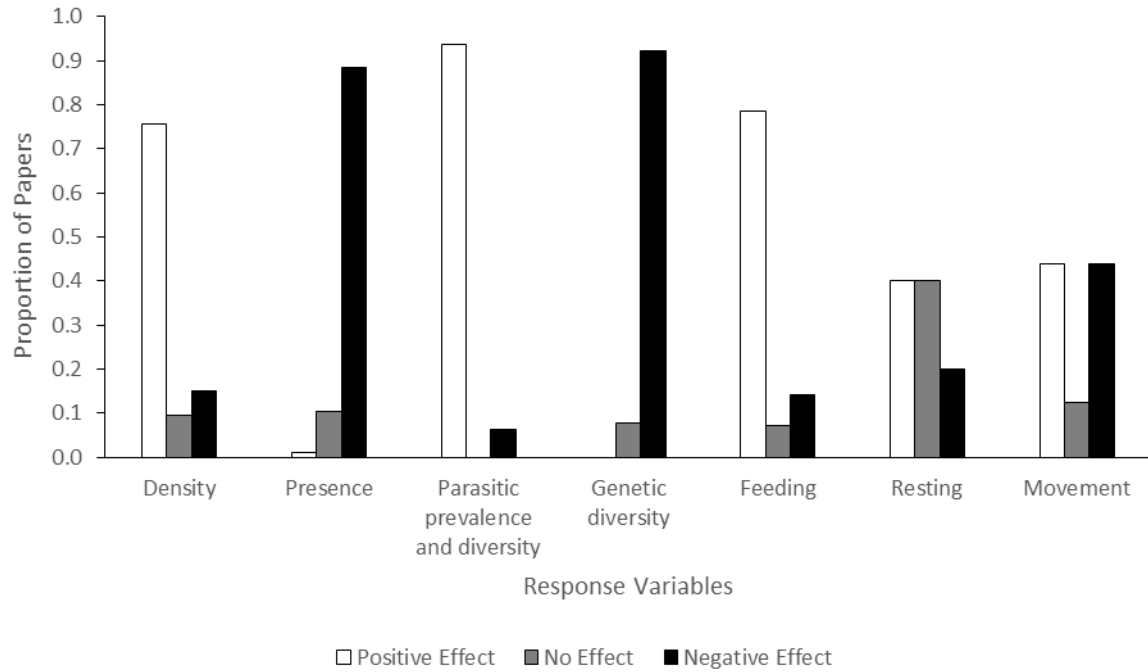
only on one primate species and few focus on multiple species. No studies on the response of multiple species were found for Madagascar.



**Figure 4 Proportion of papers and primate species per paper which evaluate habitat loss and fragmentation effects across continents (Total of papers: Neotropics: 79 (61 papers studying one species and 18 papers studying multiples species; Madagascar: 13 (all papers studying one species); Africa: 28 (21 papers studying one species and 7 papers studying multiple species; and Asia: 15 (10 papers studying one species and 5 papers studying multiples species)).**

## General Patterns

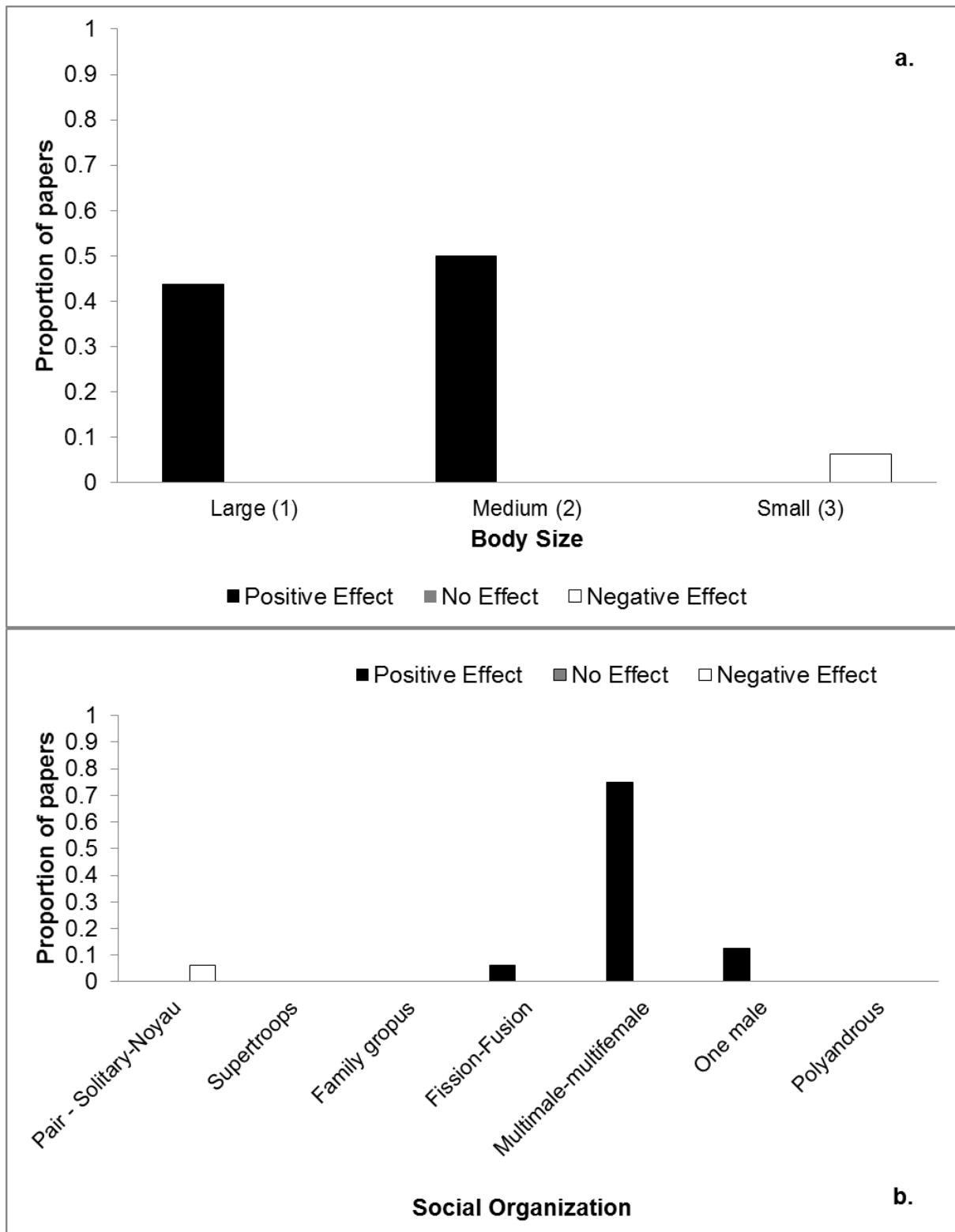
The effect of a reduction of patch size on density, presence, parasites, genetics and feeding patterns was statistically different from random (Figure 5,  $p < 0.05$ ). However, patterns for resting and movement were not significantly different from random (resting:  $p = 0.78$ ; movement:  $p = 0.24$ ). Primarily, positive effects were observed for density, parasitic prevalence and diversity and feeding while negative effects were observed for genetic diversity and presence. These were all consistent with our hypotheses. The patterns for resting and movement behaviour showed both positive and negative effects.



**Figure 5 Patch size effects on the response variables studied ( $X^2 = 11.45$ , df 6,  $p < 0.1$ ).**

## Traits

The response of density, presence, genetics and behaviour to a reduction of patch size did not show statistically significant relationships with trait values (Figure 1, Appendix C). Therefore, the available evidence was insufficient to confirm any of our hypotheses with respect to trait effects for these response variables. On the other hand, the relationship between the effect of a reduction of patch size on parasitic prevalence and diversity variation with trait values was found to be statistically significant for body size and social structure (Table 4). Contrary to our hypotheses that body size and social structure do not influence the magnitude of the effect of patch size we found that: (1) species with small body size were less susceptible to the effect of a reduction of patch size on parasite infestations than large and medium size species (Figure 6a), and (2) solitary species were less susceptible to the effect of reduction of patch size on parasite infestations than species with other social structures (Figure 6b).



**Figure 6** Effect of patch size on parasitic prevalence and diversity across primate species traits that were significant: a) social structure ( $X^2 = 6.94$ , df 2,  $p < 0.01$ ), and b) body size ( $X^2 = 16.00$ , df 3,  $p < 0.01$ ).

**Table 4. Chi-squared tests for association between each response variable and traits.**

Responses	Traits					
	Dispersal Ability	Body Size	Diet Specialization	Home Range Size	Group Size	Social Structure
Density	$X^2 = 3.21$ df = 4 $p = .5227$	$X^2 = 5.24$ df = 4 $p = 0.2636$	$X^2 = 6.07$ df = 6 $p = 0.4159$	$X^2 = 2.95$ df = 2 $p = 0.2283$	$X^2 = 1.21$ df = 2 $p = 0.5470$	$X^2 = 5.28$ df = 8 $p = 0.7276$
Presence	$X^2 = 6.43$ df = 4 $p = 0.1691$	$X^2 = 6.94$ df = 4 $p = 0.1389$	$X^2 = 3.51$ df = 6 $p = 0.7427$	$X^2 = 2.09$ df = 2 $p = 0.3524$	$X^2 = 0.95$ df = 2 $p = 0.6207$	$X^2 = 6.34$ df = 12 $p = 0.8978$
Parasitic prevalence/ Parasitic diversity	$X^2 = 0.36$ df = 2 $p = 0.8371$	$X^2 = 16.00$ df = 2 $p = 0.0003^*$	$X^2 = 4.61$ df = 2 $p = 0.0992$	$X^2 = 1.37$ df = 1 $p = 0.2416$	$X^2 = 3.20$ df = 1 $p = 0.0736$	$X^2 = 16.00$ df = 3 $p = 0.0011^*$
Genetic diversity	$X^2 = 0.09$ df = 1 $p = 0.7638$	$X^2 = 1.26$ df = 2 $p = 0.5316$	$X^2 = 2.44$ df = 2 $p = 0.2956$	$X^2 = 0.48$ df = 1 $p = 0.4878$	$X^2 = 0.93$ df = 1 $p = 0.3352$	$X^2 = 3.61$ df = 2 $p = 0.1644$
Feeding (% time, items consumed)	$X^2 = 0.29$ df = 2 $p = 0.8634$	$X^2 = 2.43$ df = 4 $p = 0.6565$	$X^2 = 3.37$ df = 4 $p = 0.4975$	$X^2 = 2.91$ df = 2 $p = 0.2330$	$X^2 = 4.50$ df = 2 $p = 0.1056$	$X^2 = 1.04$ df = 4 $p = 0.9035$
Resting (% time)	n.a.	$X^2 = 4.17$ df = 4 $p = 0.3839$	$X^2 = 7.25$ df = 4 $p = 0.1233$	$X^2 = 3.00$ df = 2 $p = 0.2231$	$X^2 = 0.48$ df = 2 $p = 0.7881$	$X^2 = 2.50$ df = 4 $p = 0.6446$
Moving (% time, daily distance)	$X^2 = 4.75$ df = 4 $p = 0.3142$	$X^2 = 5.88$ df = 4 $p = 0.2085$	$X^2 = 1.12$ df = 4 $p = 0.8918$	$X^2 = 1.20$ df = 2 $p = 0.5496$	$X^2 = 1.37$ df = 2 $p = 0.5037$	$X^2 = 6.00$ df = 6 $p = 0.432$

\*significant at  $p < 0.05$ . n.a.: Not enough data to apply statistics

## **Discussion**

### **Contributions of this paper**

For primates, we found consistent and general responses to a reduction of patch size for most response variables, but I was unable to identify strong relationships with traits, except for parasitic prevalence and diversity. This suggests that general principles for the effect of patch size on primate species may be possible, but may need more information to understand the role of traits in explaining any variation in responses among species. This is particularly important for primates because of their high sensitivity to habitat loss and fragmentation (Chapman et al. 2006a, 2010; Boyle & Smith 2010b; Arroyo-Rodriguez et al. 2013b). However, variation in their responses may limit the extent to which general principles for their conservation can be developed (Chapman et al. 2006a, 2006b). In addition, it is possible that I did not detect variation across traits because I was only able to characterise responses qualitatively (positive, negative, none), which was a limitation for my analysis. However, this limitation highlights the importance of defining clear predictors of habitat loss and fragmentation in the design of future primate studies. On the other hand, studies describing the landscape context, edge effects (Laurence et al. 2007) and additional processes such as source-sink dynamics, complementation and supplementation processes (Dunning et al. 1992) that allows primate species to survive in fragmented landscapes are needed.

My review provides two important insights. First, it appears to have good evidence for consistent directions on the overall effects of patch size on primates for a number of response variables. Second, there was not strong evidence for the influence of traits on the effect of patch size, but their effects may be masked by other confounding processes such as type of clearing, climate, hunting pressure and the qualitative nature of the data. However, this review also highlights an absence of attempts to separate the effects of habitat loss from fragmentation, with studies conducted at the landscape rather than the patch scale.

### **Synthesis of key processes**

Most response variables showed consistent patterns of increase or decrease across studies, but I was unable to find evidence for strong relationships between traits and

the response of primates to a reduction in patch size in most cases (except for parasitic prevalence and diversity). For primates, only two studies in fragmented landscapes had evaluated primate species traits as variables useful for predicting primate species presence but these had contradictory findings (Onderdonk & Chapman 2000; Boyle & Smith 2010b). Onderdonk & Chapman (2000) failed to find evidence that home range size, body size, group size and degree of frugivory were variables useful for predicting six primate species' ability to live in forest patches in Africa. Conversely, Boyle & Smith (2010b) found that the proportion of fruit in each primate species' diet (diet specialisation) was the best predictor for finding species in fragments, followed by home range size as the second best predictor, for a primate community in the Brazilian Amazon. The diversity and complexity of traits and their possible interactions in primate species may make it difficult to generalise about the role of traits in fragmented landscapes. In addition, there may be difficulties trying to lump African primates and South American primates because of the long evolutionary history that separates them (at least 35-36 My) and the ecological differences between the forest ecosystems of the two continents (Emmons & Gentry 1983). Disentangling the role of traits is important for conservation efforts at landscape and larger scales (Onderdonk & Chapman 2000; Boyle & Smith 2010b; Vetter et al. 2011). Research on multiple species with variable life history traits inhabiting fragmented landscapes will help to better understand the varying responses of primates to habitat loss and fragmentation. Studies to do this need to simultaneously control for the habitat loss, fragmentation and spatial configuration effects on the species studied, following a landscape approach to sustainable conservation (Wiens 2009).

A consistent pattern across studies was that a decrease in patch size results in a decrease in presence, but an apparently contradictory increase in density of primates (Harcourt & Doherty 2005; Benchimol & Peres 2013). This may result from processes of extinction and competition among primate species. Under habitat loss and fragmentation some species will become locally extinct and therefore their presence reduced (Chapman et al. 2006a, 2007). Subsequently an increase in density for the remaining primate species may be explained by a density compensation effect (McArthur et al. 1972) due to a reduction in inter-specific competition. Similar effects are seen in primate communities with different degrees

of hunting pressure, in which the remaining primate species increase in abundance, offset by the absence of interacting competitors (Peres & Dolman 2000). Another possibility is that this is a result of crowding in small patches (Anderson et al. 2007a; Wagner et al. 2009; Chagas & Ferrari 2011; Carretero-Pinzon 2013a) prior to the extinction debt being realised which may be evident only after several generations have passed (Chapman et al. 2006a, 2006b, 2010, 2013). This highlights the need for long-term studies in fragmented areas to disentangle these processes before and during the fragmentation process.

### **Parasitic prevalence and diversity**

One trait effect I was able to identify was that of body size and social structure for determining the effect a reduction of patch size has on parasitic prevalence and diversity. In particular, increases in parasitic prevalence and diversity due to a decrease in patch size for solitary species (noyau and solitary) were less evident than for species with other social structures. Noyau is a type of social structure in which an individual male has a large home range, including the home range of several females and their immature (Fleagle 1999). The increase in parasitic prevalence and diversity for primate species could be explained by more contact between individuals in a reduced area under habitat loss and fragmentation, with the effect being particularly strong for non-solitary species (Gillespie & Chapman 2006, 2008; Goldberg et al. 2008; Mbora & McPeck 2009; Cristobal-Azkarate et al. 2010). Habitat loss and fragmentation affects resource availability for primates, and therefore also may affect their immune reactions to parasitic infections due to nutritional stress (Gillespie & Chapman 2006, 2008). Larger primate species require more resources compared to small primate species, making them more susceptible to nutritional stress and potentially to higher parasitic prevalence and diversity as shown from the evidence in the literature (Jason & Chapman 1999; Gillespie & Chapman 2006, 2008). In conservation terms, this means that larger species may be under a greater pressure of increased parasitic prevalence and diversity, and this needs to be considered when implementing management actions in fragmented landscapes. For example, in fragmented landscapes where large primate species are present and the potential for inter-and intra-specific parasitic transmissions is high, the implementation of corridors between fragments needs to take in

consideration the matrix permeability. In addition, in fragmented landscapes, these transmissions can be increased if the nutritional stress of these species cannot be reduced.

### **Research Gaps and future directions**

Primate species living in fragmented landscapes also face additional pressures due to their close proximity to human settlements and production activities such as agriculture. These pressures can confound predictions of the effects of habitat loss and fragmentation on primate species. Management of these additional pressures is difficult because they sometimes occur concomitantly. Spatial modelling analysis and landscape-scale studies (e.g. multiple scale analysis) in fragmented areas could help to elucidate the effects of these additional confounding pressures. For example, spatial modelling analysis evaluating the movements of multiple primate species stratified by life history traits in agricultural areas, while controlling for habitat loss and degree of fragmentation, could be useful for detecting the effects of some of those additional pressures such as close proximity to human settlements. In addition, the assessment of the effect of hunting pressure and/or selective logging on fragmented landscapes may also be possible with a spatial modelling approach using multiple landscapes in which the amount of habitat and degree of fragmentation is controlled while the hunting pressures vary. I only found one study which evaluated hunting pressure and timber extraction in a fragmented landscape while incorporating patch and landscape variables to determine occupancy of primate and carnivore species for one landscape (Michalski & Peres 2005). Michalski & Peres (2005) found that timber extraction and hunting pressure have detrimental effects on primate and carnivore persistence, over and above patch size for some species' persistence.

Research applying a landscape approach to evaluating the independent effects of habitat loss and fragmentation (Arroyo-Rodriguez et al. 2013a) and including the spatial configuration of the habitat available is a priority for primate conservation. The incorporation of concepts and research designs from disciplines such as landscape ecology and spatial ecology will be particularly useful for achieving this. Importantly, understanding the role of traits on the effect of habitat loss and fragmentation is critical for making general recommendations for primate conservation in fragmented



landscapes. We therefore also recommend a greater focus on explicitly testing the role of traits in driving the responses of primates to habitat loss and fragmentation. The ability to make generalizations based on species' traits such as body size or group size could help to predict the responses of different species to landscape change and management actions (e.g. a corridor implementation or a restoration project). This could provide a more cost-effective output for conservation than waiting for the outcomes of the long-term monitoring of primate responses. This could mean the difference between saving or losing a primate species in rapidly transforming landscapes.

### **Chapter 3: Influence of landscape variables relative to site and patch variables for primate conservation in the Colombian Llanos**

(Submitted to Landscape Ecology)

#### **Introduction**

Deforestation continues at an alarming rate in the tropics (FAO 2011; Hansen et al. 2013). Understanding the spatial distributions of wildlife populations is important for their conservation and management, especially in tropical areas (Fahrig 2001; McAlpine et al. 2006; Fisher & Lindenmayer 2007; Elith & Leathwick 2009; Guisan et al. 2013). Species' distributions are influenced not only by the characteristics of individual patches but also by the structure and composition of the surrounding landscape (McGarigal & McComb 1995; Guisan et al. 2007; Elith & Leathwick 2009). An important consideration is the amount of suitable habitat which relates to habitat loss (Fahrig 2003; Arroyo-Rodriguez et al. 2013a) and how this affects the persistence and spatial distribution of species (With & King 1999). The effects of both habitat loss and fragmentation (breaking apart of habitat) are species-dependent and vary with the scales at which these processes are studied (McAlpine et al. 2006; Jackson & Fahrig 2012). The importance of landscape variables and its influence on spatial distribution of primate species at different scales are needed to define clear conservation strategies.

Primates are an important component of biodiversity and ecosystem function in many tropical regions. However, they are under threat from habitat loss and fragmentation (Mittermeier & Oates 1985; Rylands et al. 2008a; Schipper et al. 2008). Nonetheless, most studies focus on the effects of patch-scale fragmentation on primates and have ignored the influence of landscape composition and configuration at broader scales (Harcourt & Doherty 2005; Arroyo-Rodriguez et al. 2013a; Benchimol & Peres 2013; Arroyo-Rodriguez & Fahrig 2014; Carretero-Pinzón et al. 2015). Only a few studies have included landscape-scale (100 – 1000 ha) variables to predict the occurrence of primate species and demographic changes (Anzures-Dadda & Manson 2007; Escobedo-Morales & Mandujano 2007; Arroyo-

Rodriguez et al. 2008; Pyritz et al. 2010; Thornton et al. 2011; Arroyo-Rodriguez et al. 2013b). This is a critical limitation because species' responses to habitat loss and fragmentation are influenced by the scale at which these processes occur, and they are multi-scaled in nature (Eigenbrod et al. 2008; Smith et al. 2013; Thorton et al. 2011; Martin & Fahrig 2012; Arroyo-Rodriguez et al. 2013b). Thornton et al. (2011) and Arroyo-Rodriguez et al. (2013b) applied a multiscale approach to evaluate primate species' responses to habitat loss and fragmentation. Thornton et al. (2011) found that habitat fragmentation strongly affected Geoffroy's spider monkey (*Ateles geoffroyi*) in Guatemala, at a 500 m landscape radius. On the other hand, Arroyo-Rodriguez et al. (2013b) found that populations of the black howler monkey (*Alouatta pigra*), in Mexico, were primarily affected by changes in patch-scale attributes than landscape-scale metrics in a 500 ha landscape.

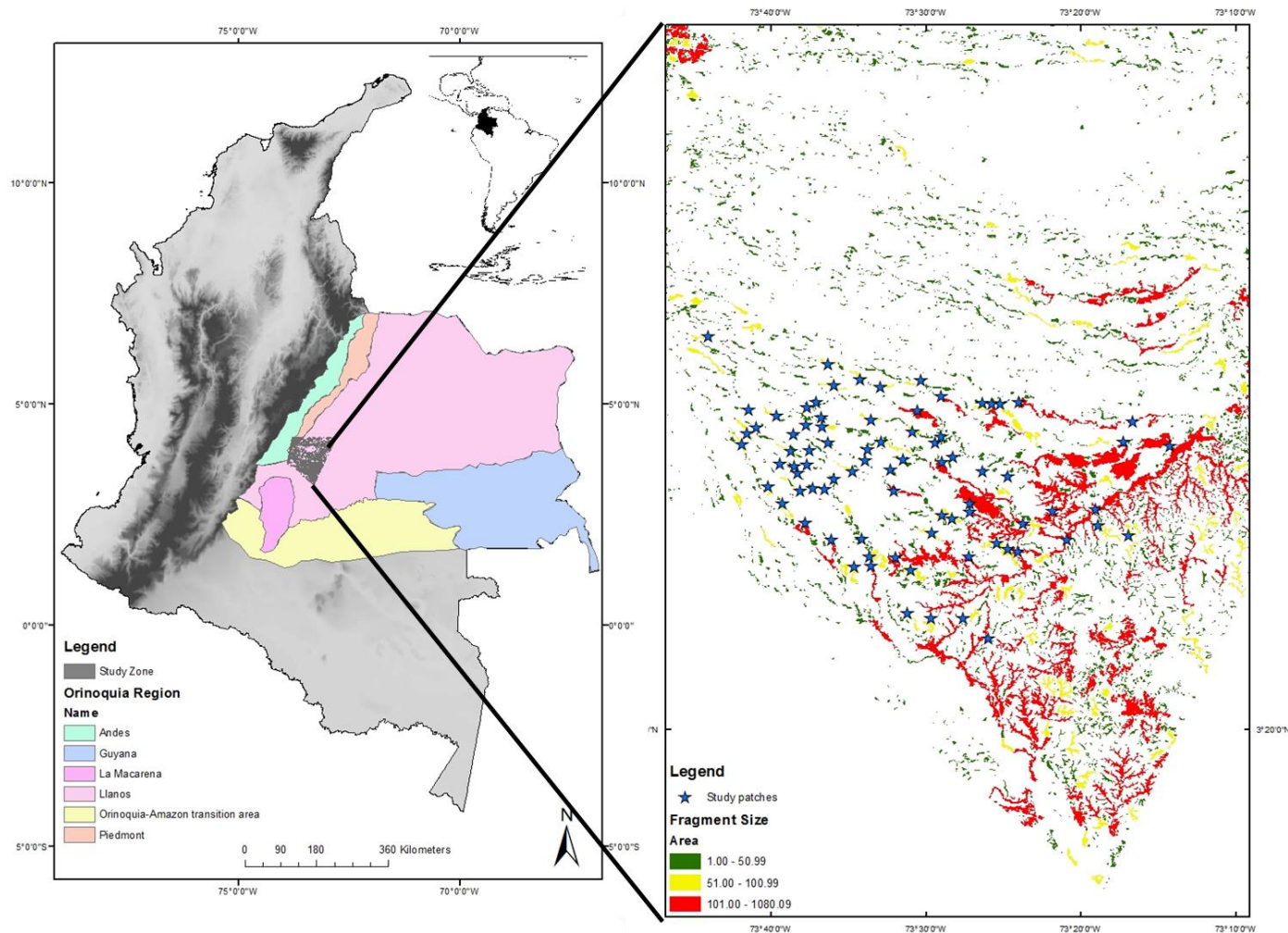
In Colombia, the main drivers of deforestation are human population growth and migration, infrastructure projects, palm oil plantations, agriculture and cattle ranching (Etter et al. 2006a, 2008; Fedepalma 2014; Ecopetrol 2015). Orinoquia (an area of 388,101 km<sup>2</sup> in size) is a region of Colombia with high rates of conversion of natural savannas and degradation of gallery forest and lowland rain forest (Etter et al. 2008). This region is part of the Orinoco River catchment (Dominguez 1998), and is an important area for primate biodiversity. The region supports from 2 - 10 primate species depending on the vegetation, including the endemic dusky titi monkey (*Callicebus ornatus*), the Brumback night monkey (*Aotus brumbacki*) and the Colombian squirrel monkey (*Saimiri cassiquiarensis albigena*) (Defler 2010). In the Orinoquia the main drivers of habitat loss and fragmentation are similar to the rest of Colombia, and includes illegal crops (Armenteras et al. 2009, 2013; Castiblanco et al. 2013). Studies evaluating the effects of habitat loss and fragmentation on primates in the Orinoquia are scarce and limited to density estimates of populations in forest fragments (Wagner et al. 2009; Carretero-Pinzon 2013a) and behavioral studies of species living in forest fragments (Zarate & Stevenson 2014). Understanding the relative influence of landscape change in the region is critical for the conservation of this diverse primate community. The region also provides an excellent opportunity to understand the multi-scale drivers of primate distributions and abundance more generally.

This study addressed the question: how important are landscape-scale forest area and configuration relative to patch-scale and site-scale habitat variables for the occupancy and abundance of four primate species in the Colombian Llanos. I used zero-inflated models to test the relative influence of landscape-scale (500-2500 m radius around forest patches), patch-scale (1 – 1080 ha) and site-scale (transect of 1 km) variables on occupancy and abundance. Occupancy and abundance of primate species in the study region are driven by landscape variables as well as the site and patch context variables collectively. Also, I found considerable variation in the scale at which landscape variables affect each species.

## **Methods**

### **Study Area**

The study was conducted in the Llanos bioregion (*sensu* Lasso et al. 2010), near the town of San Martín in the Colombian Orinoquia (Figure 7). The Llanos is characterized by lowland alluvial terraces and plains, dissected by rivers originating in the Andes or in the upland savannas and draining into the Orinoco River (Lasso et al. 2010). The vegetation is dominated by flooded and dryland savannas, gallery forest associated with drainage lines and lowland rainforest (Lasso et al. 2010). There are five primate species living sympatrically in the region: red howler monkey, dusky titi monkey, black-capped capuchin, Colombian squirrel monkey and Brumback's night monkey (Carretero-Pinzon 2013a). This study focuses on the four diurnal species.



## Survey Design

**Site selection:** Ninety forest fragments in the piedmont of the Orinoquia region were selected (Figure 1b) to address the research question. A randomly stratified survey design (Rogerson 2010) based on forest fragment size and the proportion of forest surrounding each patch at a 1000 m buffer distance were used to select potential sites for primate and vegetation surveys. This was based on a land cover map derived from a mosaic of Landsat 7 ETM images from 2000 ([www.earthexplorer.usgs.gov](http://www.earthexplorer.usgs.gov)) at a 30 m spatial resolution using a supervised classification with ArcMap 10.1 (ESRI ArcGIS 10). Four classes of land cover were identified (crops, forest, pastures and water). The classified map was then used to stratify each forest patch by area (3 classes: 1 – 50 ha, 51 – 100 ha and 101 – 1000 ha) and the percentage of forest cover surrounding the fragments at a 1000 m radius buffer (3 classes: 0 – 33 %, 34 – 66 % and > 67 %). The buffer distance took into account the dispersal distance of the target primate species (which range from 200 m – 4000 m). These distances are based on observations by Arroyo-Rodriguez & Dias (2010), Defler (2010) and Carretero-Pinzon (unpublished data). A combination of forest fragment size and percentage of forest cover surrounding the fragments (9 classes, Table 5) were used to randomly select 10 sites per habitat class with sites widely distributed across the study region. Spatial autocorrelation among fragments was avoided by selecting fragments at least 1 km apart.

**Table 5 Classification of sampling fragments according to a combination of fragment size classes and proportion of forest cover surrounding the fragments (connectivity measure).**

<b>Fragment size class</b>	<b>Proportion of forest cover classes</b>	<b>Combination Code</b>	<b>Number of potential fragments</b>	<b>Fragments sampled by combination of classes</b>
1 – 50 ha	0 – 0.33	1	5551	11
1 – 50 ha	0.34 – 0.66	2	90	10
1 – 50 ha	> 0.66	3	37	10
51 – 100 ha	0 – 0.33	4	1275	10
51 – 100 ha	0.34 – 0.66	5	77	10
51 – 100 ha	> 0.66	6	117	10
101 – 1000 ha	0 – 0.33	7	78	10
101 – 1000 ha	0.34 – 0.66	8	0	0
101 – 1000 ha	> 0.66	9	14	10

Landowners were contacted to obtain permission for data collection in the selected survey sites. Selected sites more than 60 km from the focal area of San Martin that were near areas of conflict (guerrillas) were eliminated for logistical and security reasons. The eliminated sites were replaced with alternative sites using the same criteria of selection (combinations of fragment size and proportion of forest around focal fragments). The final set of selected fragments were then evaluated in the field for a minimum canopy height. Fragments with canopies less than 10 m in height were considered regenerated or regrowth forest and were not included in the study, as we focussed on primary forest. Classified forest fragments that now are palm oil plantations were eliminated, this was verified in the field by direct observation. All the pre-selected areas eliminated were replaced by fragments of

the same categories as the ones eliminated, and at least 1 km from fragments already sampled. A total of 81 fragments were surveyed including all the combination classes present in the area (Table 5).

A minimum of one transect, 1 km in length, was located randomly in each fragment. Transect direction was randomly chosen. Where possible, transects were straight, but in fragments with irregular shapes, the direction changed according to the fragment form. A total of 83 transects were surveyed, one transect for each fragment, except the largest fragment which had three transects.

### **Primate surveys**

Count data were collected by recording every primate group and individual of each species observed along a transect. Counts were collected by establishing the number of individuals per group. Counts were conducted from 0600 to 1100 hours and again at 1330 to 1630 hours on the same day, and repeated on consecutive days. Each transect was surveyed three to six times, with a minimum of three surveys per transect for all fragments. Surveys were not conducted in heavy rain. Transects were walked at approximately 0.5 km/h with only diurnal primate species recorded. When a primate group was visually detected, a minimum of 15 minutes was taken to count the group members and determine group composition (number of males, females and immature). The time of detection was also recorded. The coordinates of each observation were registered using a GPS. All observations and species identifications were aided by binoculars, and primate species classification followed Defler (2010), Ruiz-Garcia & Castillo (in prep.) and Mittermeier et al. (2013). Primate surveys were carried out by the first author.

### **Vegetation surveys**

For each transect, vegetation surveys were conducted in four 10 x 50 m plots, located every 250 m along the 1 km. For each plot, all trees with a diameter at breast height (DBH) >10 cm were recorded to species level and measured. The presence of trees with fruits, flowers and young leaves was recorded. The number



of stumps cut by humans, and the respective DBH were recorded. Species identifications were based on vegetative and reproductive material using the guide “Guia de frutos de La Macarena” (Stevenson et al. 1998) as well as expert identification by Francisco Castro. The percentage of canopy cover (calculated from a white and back picture, Phoonjampa et al. 2011) and canopy height were recorded from one single point every 200 m along the transect. Presence of natural fence rows (defined as tree-lines used to separate adjoining pastures, Carretero-Pinzon et al. 2010) and classification of the surrounding matrix were recorded by direct observation for each fragment. The landscape matrix surrounding the forest fragments was categorised as *pastures* (including introduced pastures or natural savannahs) and *plantations* (crops and palm oil plantations, alone or combined with exotic pastures). Vegetation surveys were done by the first author with the assistance of Francisco Castro (Botanist of Los Llanos University), an expert on the local flora

### **Variable selection**

A combination of ecologically-relevant site-scale, patch-scale and landscape-scale variables was selected, based on a review of the primate literature (Table 6). Eight site-scale variables were selected canopy cover, canopy height, basal area, number of food trees, number of stumps, presence of trees with, fruits, flowers or young leaves. Four patch-scale variables were also selected, patch size, patch shape index, presence of natural fence rows and type of matrix. Two landscape-scale variables were selected, percentage of forest cover and patch density. Site-scale variables were measured along the 1 km transect, patch-scale variables were measured for the whole patch where the transect was located, and landscape-scale variables were measured at three buffer distances (500 m, 1000 m, and 2500 m) surrounding each forest fragment. Buffer areas were calculated with ArcMap 10.1 (ESRI ArcGIS 10). The buffer distances were based on the relevant primate literature and observational information available of minimum dispersal distances (500 m, *Callicebus*), average (1000 m for all species) and

maximum dispersal distance (2500 m, *Alouatta*) (Arroyo-Rodriguez et al. 2013b, Carretero-Pinzon, unpublished data). The map with selected fragments was further corrected using a forest and non-forest map of Colombia produced by IDEAM (2014) that is based on satellite images from 2010, for more precision on land cover classification and fragment sizes.

## **Statistical Analysis**

To model the occupancy and abundance of each species, I used zero-inflated Poisson generalized linear models (Lambert 1992; Martin et al. 2005; Zuur et al. 2009; Rhodes 2015). These models have an occupancy component and an abundance component, given occupancy, and are ideally suited for dealing with zero-inflated count data (Martin et al. 2005; Rhodes 2015). They also allow the simultaneous modelling of occupancy and abundance because the models consist of a mixture of an occupancy process and an abundance process (Lambert 1992; Martin et al. 2005; Zuur et al. 2009; Rhodes 2015). Each species was modelled separately and the response variable was the number of individuals per transect. We modelled the occupancy and abundance components of the models as functions of the site, patch and landscape variables with variation in sampling effort controlled for in the models as an offset (Zeileis et al. 2008). We formulated several hypotheses and tested the support for these based on an information theoretic approach (Burnham & Anderson 2002). We hypothesized that both occupancy and abundance of each primate species were influenced by variables at only one scale (only site-scale, only patch-scale or only landscape-scale) or by a combination of two scales (site and patch scale, site and landscape scale or patch and landscape scale) or by the variables at all scales combined. We assumed that the same variables influence occupancy and abundance of the species studied. These models were evaluated for the 500 m, 1000 m, and 2500 m landscape buffer distances for the landscape variables.

**Table 6 Summary of site, patch and landscape variables selected from primate literature as predictive variables of primate occupancy and abundance.**

<b>Variable Name</b>	<b>Description</b>	<b>Reference</b>
<b>Landscape Scale</b>		
Patch density	The number of patches present divided by the area of the buffer (500 m, 1000 m and 2500 m).	McAlpine et al. 2006; Arroyo-Rodriguez et al. 2013b
Percentage of forest cover	Percentage of forest present in each buffer area (500 m, 1000 m and 2500 m)	Arroyo-Rodriguez et al. 2013b
<b>Patch Scale</b>		
Patch size	Size in hectares of each fragment surveyed	Arroyo-Rodriguez et al. 2013b
Patch Shape Index	Index of patch shape complexity	Forman & Godron 1986; Arroyo-Rodriguez et al. 2013b
Matrix type	Presence of crops, African palm oil plantations and pastures surrounding the focal fragment. Only two categories were used for the analysis: pastures (includes natural savannahs and small crops) and African palm oil plantations	Anderson et al. 2007b; Blair & Melnick 2012
Presence of natural fence rows	Presence of natural fence rows (unplanted lines of native trees left standing during forest clearance to divide pastures)	Carretero-Pinzón et al. 2009, 2010
<b>Site Scale</b>		
Average Percentage of Canopy Cover	Canopy cover pictures at 1.5 m from the ground with a Coolpix 100 digital camera, every 200 m on each transect (six pictures per transect)	Wieczkowski 2004
Average Canopy	Canopy height measure taken with a digital	Pozo-Montuy et al.

Height	range finder every 200 m in each transect	2008; Anzures-Dadda & Mason 2007
Number of stumps	Number of stumps cut by humans found in each vegetation strip on each transect (4 strips by transect)	Chapman et al. 2007
Tree density	Number of trees per hectare for each vegetation strip in each transect	Chapman et al. 2010
Number of plant species by transect	Number of plant species for all strips in each transect	Chapman et al. 2010
Presence of trees with fruits, flowers or young leaves	Number of trees with fruits, flowers or young leaves present at the moment of the vegetation surveys, in all strips in each transect	Chapman & Onderdonk 1998
Basal area per transect	Basal area of all plant species found in all strips in each transect	Chapman et al. 2006b
Number of food plants consumed by primate species by transect	Number of all plant species consumed by each primate species found in all strips in each transect	Chapman et al. 2006b <sup>1</sup>
Basal Area of food plants consumed by primate species by transect	Basal area of all plant species consumed by each primate species found in all strips in each transect	Chapman et al. 2006b <sup>1</sup>

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<sup>1</sup>The list of plant species consumed by each primate species studied here was based on the following references by primate species: *Alouatta seniculus*: Escudero 2005, Beltran 2005, Santamaria 2005, Ramos 2007; *Sapajus apella*: Torres 2005, Ramos 2007, Fragaszy et al. 2004b, Gomez-Posada 2012a, 2012b; *Saimiri cassiquiarensis albigena*: Carretero-Pinzon 2000, 2008; *Calliebus ornatus*: Ospina 2006.

All statistical analysis was performed using the R software ([www.r-project.org](http://www.r-project.org)) and the package `pscl` (Zeileis et al. 2008). I ranked all models for each species and according to their AIC values and calculated their Akaike weights (Burnham & Anderson 2002). For each species, a 95% confidence set of models was constructed using the cumulative Akaike's weight for each model, starting with the highest and adding the next model until the cumulative sum of weights exceeded 0.95 (Burnham & Anderson 2002, see R Code in Appendix D). In addition, the relative importance of each set of variables (site-scale, patch-scale and landscape-scale) was calculated to evaluate the magnitude of the effect of a variable on the occupancy and abundance responses of each primate species.

To test for spatial autocorrelation among model residuals, I created spline correlograms using the `ncf` package in R for best models (Bjørnstad 2013). Spline correlograms display the spatial correlation using a smoothed spline with 95% confidence intervals calculated by bootstrapping (Bjørnstad & Falck 2001). Splines that are flat and centred on zero demonstrate spatial randomness (i.e., the data are spatially independent), while splines that are not flat with 95% confidence intervals that do not overlap zero indicate spatial autocorrelation (Bjørnstad & Falck 2001).

## Results

All four species were detected in 22 % of the patches surveyed. Only 1 % of the patches surveyed did not have a primate species present. A total of 271 dusky titi monkeys, 627 howler monkeys, 1092 black-capped capuchin monkeys and 2799 Colombian squirrel monkeys were observed, including adults and immature (sub-adults, juveniles and infants), and females and males.

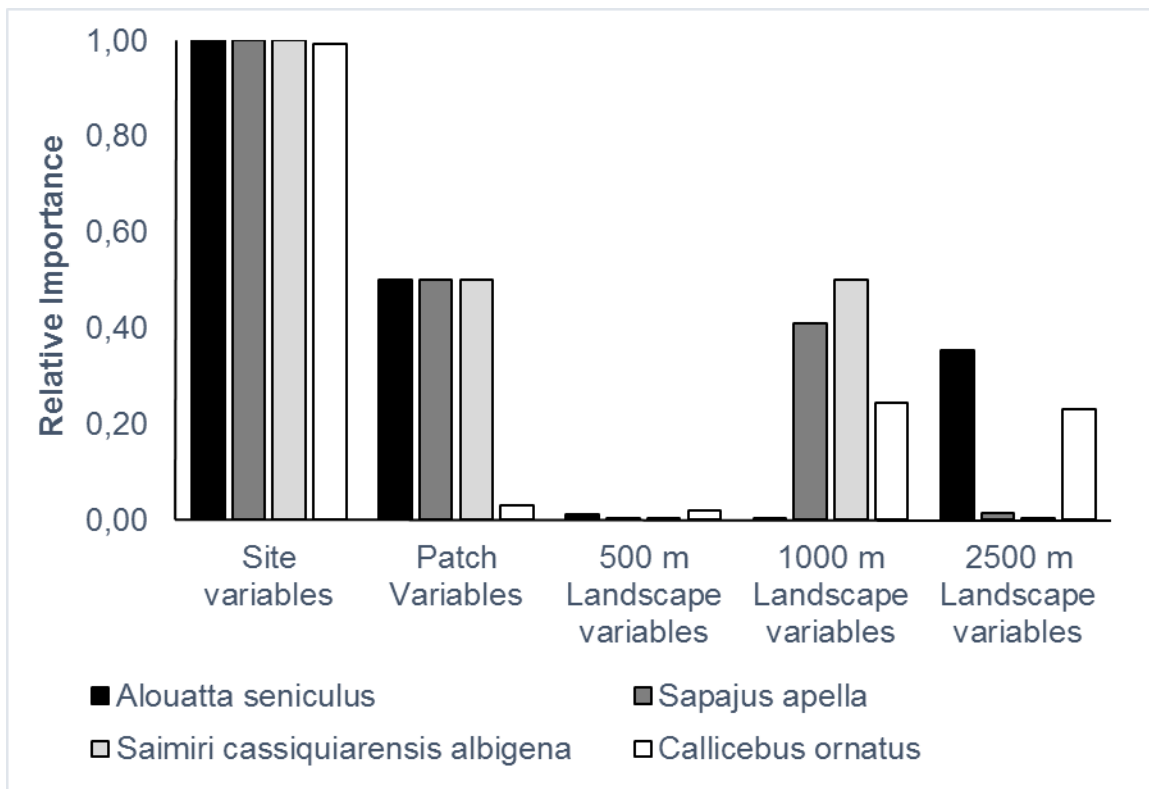
The 95% confidence set of models showed low model uncertainty with all species represented by only one or two models, except for the dusky titi monkey, which contained four models (Table 7). The best models explaining the occupancy and abundance of black-capped capuchin and Colombian squirrel monkey contained variables at the site, patch and 1000 m landscape spatial extent. Whilst the best model explaining occupancy and abundance of the red howler monkey contained

variables at the site, patch and 2500 m landscape spatial extent. Models with site-scale and 1000 m and 2500 m landscape-scale variables performed best for the models of the occupancy and abundance of the dusky titi monkey. There was no evidence of spatial autocorrelation in the model residuals for any of the best models (Appendix D).

**Table 7 Distribution model ranking, Akaike information criteria (AIC) for the 95 % confidence set of models for four primate species in Colombian Llanos.**

Rank	Model name	AIC	$\Delta_i$	$w_i$
<b>Red howler monkeys (<i>Alouatta seniculus</i>)</b>				
1	All variables 2500m	644.19	0	0.707
2	All site and patch variables	646.13	1.94	0.268
<b>Dusky titi monkey (<i>Callicebus ornatus</i>)</b>				
	All site and landscape variables			
1	1000m	376.05	0	0.48
	All site and landscape variables			
2	2500m	376.32	0.27	0.42
3	All variables 2500m	381.33	5.28	0.034
	All site and landscape variables			
4	500m	382.24	6.19	0.022
<b>Black-capped capuchins (<i>Sapajus apella</i>)</b>				
1	All variables 1000m	1265	0	0.821
2	All site and patch variables	1268.3	3.36	0.153
<b>Colombian squirrel monkey (<i>Saimiri cassiquiarensis albigena</i>)</b>				
1	All variables 1000m	2095.7	0	0.999

The importance of the landscape-scale variables, although was important for three of the species studied, was not as strong as the relative importance of the site-scale variables, but similar to the patch-scale variables for all the study species (Figure 8), except for dusky titi monkeys. For this species, the landscape-scale variables had a stronger effect than patch-scale variables, but weaker than site-scale variables.



**Figure 8 Relative importance of site, patch and landscape scale variables for each primate species studied.**

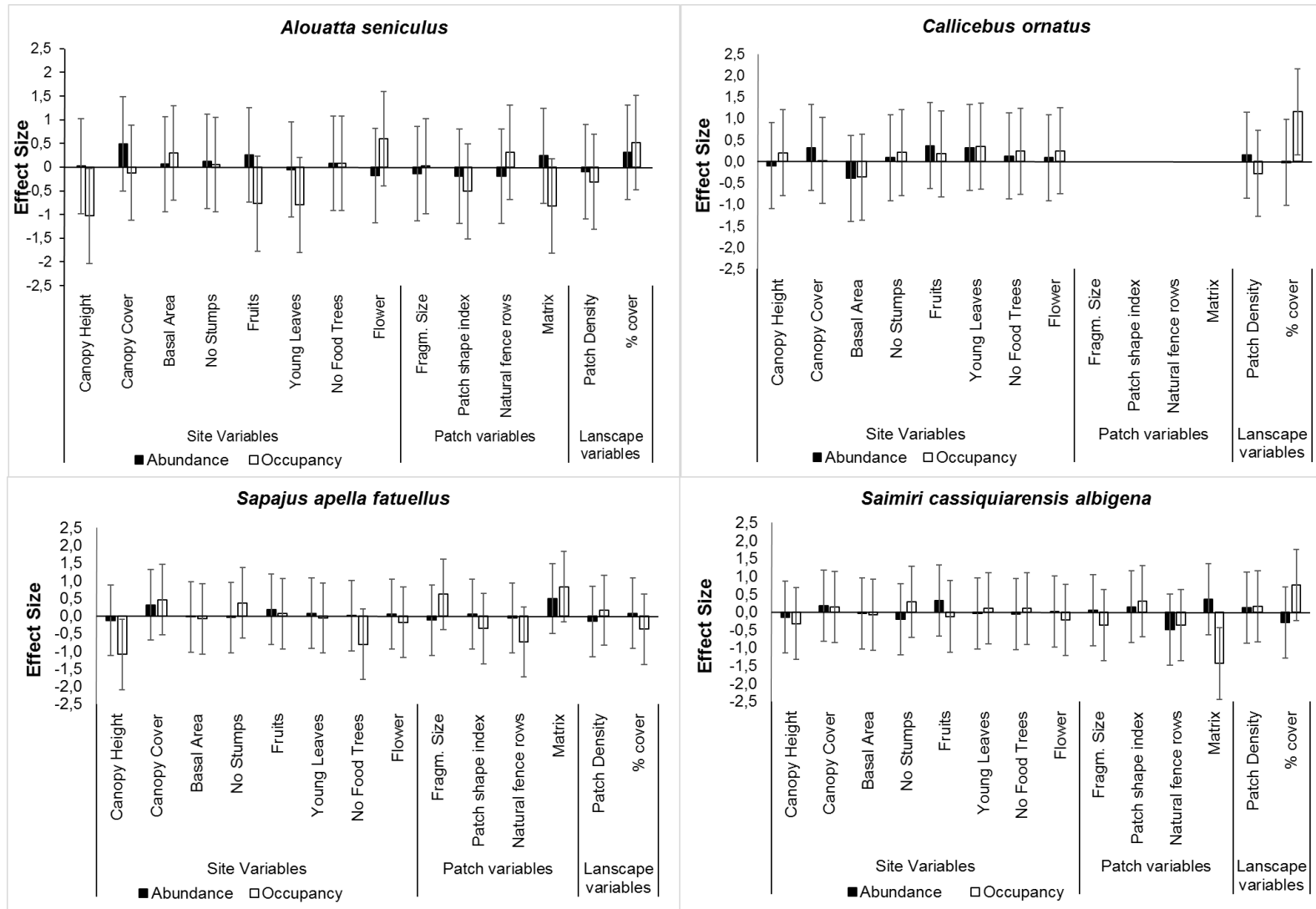
The occupancy and abundance of primate species were influenced by variables of all scales but with some differences among species (Figure 9). Red howler monkey occupancy was influenced negatively by canopy height and presence of trees with young leaves and fruits at the site-scale and the patch context (palm oil plantations in the matrix) and patch shape, while abundance was positively influenced by canopy cover, presence of trees with fruits and the percentage of forest cover at the landscape scale. Black-capped capuchin occupancy was negatively influenced

by canopy height and number of food trees at the site scale and positively by the patch context (palm oil plantations), while abundance for this species was positively influenced by canopy cover at the site scale and the patch context (palm oil plantations). The Colombian squirrel monkey occupancy was negatively influenced mainly by patch context (palm oil plantations) and positively by the percentage of forest cover in the landscape, while its abundance was influenced only by patch context (negatively by absence of natural fence rows and positively by palm oil plantations as type of matrix). Finally, dusky titi monkey occupancy was positively influenced by the percentage of forest cover, while its abundance was negatively influenced by basal area and positively by the presence of trees with fruits and young leaves.

## **Discussion**

The findings of this study highlight two important considerations when evaluating the effects of landscape change on primate occupancy and abundance. First, landscape variables as well as the site and patch context variables collectively influence the way in which primate species are distributed spatially in fragmented landscapes. Secondly, there is considerable variation in the scale at which landscape variables affect each species, which is consistent with differences in the dispersal distances known for the study species.





**Figure 9** Effect size for the model with the highest Akaike weight for all primate species studied.

This study applied a landscape approach to understand the patterns of occurrence and abundance of four primate species in Colombia. It has broader implications for understanding the effects of landscape change on other primate species in Neotropics and elsewhere. My results are consistent with two of the main concepts in landscape ecology theory: context and scale (Wiens 2009). The spatial context surroundings a patch matters (Wiens 2009), as it is illustrated by the influence of matrix type and presence of natural fence rows for occupancy of red howler monkeys, black-capped capuchins and Colombian squirrel monkeys. In addition, it demonstrates the need to focus on the scales that are appropriate for the organisms to understand the interaction between populations and landscape pattern (Wiens & Milne 1989; Turner et al. 2001; Wu & Li 2006; Wiens 2009). This is illustrated by the difference in scale for the species of study. In addition, our results are consistent with the findings of Thornton et al. (2011) and Arroyo-Rodriguez et al. (2013b) which also highlight the importance of the scale to understand the spatial distribution of other Neotropical primates. Below I expand on main inferences for key ecological process for the species studied here.

### **Key landscape processes**

This study highlights the need to explicitly consider the structure of whole landscapes in primate studies evaluating the effects of habitat loss and fragmentation on their occupancy and abundance. The percentage of forest cover influences occupancy and abundance of red howler monkeys, Colombian squirrel monkeys and dusky titi monkeys. The influence of this measure of habitat loss for other primate species has been reported by Arroyo-Rodriguez et al. (2008). In that study, they compared landscapes with different spatial configurations identifying a positive correlation between the total amount of forest and the occurrence of Mexican mantled howlers (*Alouatta palliata mexicana*). In my study, the negative weak effect of percentage of the forest cover on the black-capped capuchins can be explained by their ability to utilise the matrix as well as their diet flexibility and adaptability to different habitats, typical of other species of tufted capuchin monkeys (= *Sapajus* spp.; Chiarello 2003; Fragaszy et al. 2004a, c; Pyritz et al.

2010). The importance of the matrix varies among species with some species such as black-capped capuchins able to utilise the matrix, while other species such as red howler monkeys are negatively affected by matrix elements such as palm oil plantations. This is consistent with differences in species life history such as diet and home range sizes. The space requirement between these species is different, with higher home range sizes for capuchins compared to howler monkeys (Defler 2010). In fragmented landscapes, black-capped capuchins are forced to use the matrix to cross between patches in search of food (Carretero-Pinzón, pers. obs.). The increase in the probability of occupancy observed for the black-capped capuchin when palm oil plantations occurs in the matrix is consistent with this species consumption of palm nuts (Carretero-Pinzón, pers. obs.) and their flexibility in using and crossing different types of matrix common in species of tufted capuchins (Jack & Campos 2012). Palm oil plantations also influenced the abundance red howler monkeys, black-capped capuchins and Colombian squirrel monkeys. Only one previous study has evaluated the effect of palm oil plantations on Neotropical primate gene flow (Blair & Melnick 2012). That study found, that palm oil plantations can act as moderate barrier to gene flow of the Central American squirrel monkeys (*Saimiri oerstedii*), and its effect is evident only during long distance dispersal events (Blair & Melnick 2012).

An interesting result for all the species studied was that fragment size was not important, contrary to the findings of other studies (Cristobal-Azkarate & Arroyo-Rodriguez 2007; Anzures-Dadda & Manson 2007; Arroyo-Rodriguez et al. 2008; Arroyo-Rodriguez et al. 2013b). The species studied here are a subset of all primate species present in the Llanos. They are typical of gallery forest of the Colombian and Venezuelan Llanos and adapted to other divergent habitats, but they also persist in areas that are naturally fragmented, such as gallery forest (Carretero-Pinzon & Defler in press). Their adaptation to edge habitats explains their long history of presence in this type of habitat and may have influenced their persistence in anthropogenic forest fragments typical of the study region. The study species that use the ground for feeding or movement are more able to better adapt to habitat loss and fragmentation with only slight modifications of their

behavioural ecology (Fragaszy et al. 2004a, c; Pozo-Montuy & Serio-Silva 2007; Bicca-Marques et al. 2009). However, the increased isolation and degradation of the remaining fragments in the region are affecting the forest structure and resource availability, increasing the pressure on the persistence of these primate species. This region is one of the main colonization frontiers and one of the main areas for expansion of petroleum resource developments, palm oil plantations and cattle ranching in Colombia (Ecopetrol 2015; Fedepalma 2014).

### **Site-scale processes**

The findings of this study highlights the importance of site-scale variables in explaining primate occupancy and abundances. Site-scale variables are related to forest structural attributes such as canopy height and canopy cover and measures of resource availability such as number of food trees and the presence of trees with fruits, flowers or young leaves. However, the influence of these variables varied unexpectedly among species. For example, a strong negative effect of canopy height on the occupancy of red howler and black-capped capuchin monkeys was unexpected. Canopy height has been used as a measure of forest quality for species of *Alouatta* (*A. palliata*, Anzures-Dadda & Manson 2007; *A. pigra*: Pozo-Montuy et al. 2008). However, this interpretation may not be true for other types of forest which have different canopy heights. The negative effect observed in our study can be related to the variable canopy height characteristic of Colombian Llanos forests (range from 10-25 m in height), which does not necessarily relate to habitat quality but rather to other features such as topography and forest composition (Lasso et al. 2010). Another example of a variable that I did not expect to be negative for occupancy of red howler monkeys was the presence of trees with young leaves, an important food for a folivorous primate species such as *Alouatta* spp. (Defler 2010). However, this negative effect can be related to the time of the surveys that were mostly accomplished during the dry season, when this resource is not available (Carretero-Pinzon, pers. obs.).

### **Importance of scale for primate conservation**

The scale at which the variables included here were more important for explaining the occupancy and abundance of the primate species studied varies with the species. For example, for dusky titi monkeys, black-capped capuchins and Colombian squirrel monkey variables at 1000 m are more explanatory, therefore this is the scale at which conservation strategies for these species need to be focused. For red howler monkeys, the 2500 m scale is more important and conservation strategies for this species need to be focused at this scale in the region. Only two previous studies have evaluated the scale at which variables affect the occupancy and abundance of primate species (Thornton et al. 2011; Arroyo-Rodriguez et al. 2013b), with only one study conducted on a similar species to one of the species studied here. Arroyo-Rodriguez et al. (2013b) found that black howler monkey populations are more affected by changes in patch-scale metrics and 100 ha landscape metrics than landscape metrics in a 500 ha landscape. The difference in scale at which the red howler monkeys need to be considered is larger than that found by Arroyo-Rodriguez et al. (2013b) for black howler monkeys. Although both species belong to the same genus, red howler monkeys are widely distributed and found in a greater diversity of habitat types than the black howler monkeys (Mittermeier et al. 2013), therefore this scale difference highlights the importance of caution when generalizing about scales at which the effects of habitat loss and fragmentation affect species belonging to the same genus. There are few studies that use a scaling analysis to evaluate the effect of predictive variables at different scales (Anzures-Dadda & Manson 2007; Arroyo-Rodriguez et al. 2008; Thornton et al. 2011; Arroyo-Rodriguez et al. 2013b). Primate studies therefore need to focus on multiple scales of analysis to better understand the scales at which the variables affect occupancy and abundance of those species in order to make informed decisions on population and landscape management.

## Approach and Limitations

I applied a landscape approach in this study that incorporates two main concepts of landscape ecology theory: scale and context (Wiens 2009). In fragmented landscapes, the context of the patches (i.e. matrix) in which species persist is important to determine their spatial distribution as well as the strategies to cope with the effects of habitat loss and fragmentation. My study highlights the importance that this context has on the observed occupancy and abundance of primate species. In addition, is important to choose scales that are based on the biological information we had of the species of study, such as dispersal distance. This is particularly relevant as it helps us to understand the interaction between populations and spatial pattern (Wiens & Milne 1989; Wu & Li 2006; Wiens 2009).

It is possible to make some generalizations on the site, patch and landscape variables that influence the occupancy and abundance of the species studied here. Also, it is possible to extrapolate to other areas of Colombian Orinoquia where vegetation and topography are similar, in the case of a widely distributed species such as the red howler monkey (Defler 2010). However, caution needs to be exercised in applying the same generalities to other regions because of the scale and anthropogenic factors can affect those populations in different ways. In addition, extrapolation to other primate species that are habitat- or diet-specialized, such as woolly (*Lagothrix* spp.) and spider monkeys (*Ateles* spp.), needs to be done with caution as these species depend on dense forest with higher productivity (Stevenson 2008). Seasonal use of forest fragments (Carretero-Pinzon, unpublished data) also can affect detection rates and influence inferences from occupancy and abundance models for species with high mobility in the matrix present in the study area (pastures and palm oil plantations), such as the red howler and the black-capped capuchin monkeys. An additional limitation of the models used here is that they do not account for group composition and size of primate species found in the fragments. Group composition and size affect how primate species behave and influence individual fitness (Majolo et al. 2008) and their persistence of the species in fragmented landscapes.

## **Implications for conservation**

This study highlights the importance of managing landscapes at scales relevant to target species of primates. It highlights the need to focus conservation actions on avoiding habitat loss and increasing the amount of habitat available at landscape scale to increase occupancy and abundance. This is particularly important for the two endemic species present in the study area (dusky titi monkey and the Colombian squirrel monkey) because their distributions occur in highly fragmented habitats (Carretero-Pinzón 2013b; Carretero-Pinzón et al. 2009, 2013). The threats present within the distributions of these two endemic species (cattle ranching, African palm oil plantations and petroleum resource exploration and exploitation) drive habitat loss and fragmentation at large scales (Wagner et al. 2009; Carretero-Pinzón 2013b; Carretero-Pinzón et al. 2009, 2013). Therefore, habitat area, quality and connectivity of the remaining habitat are likely to be imperative for the survival of these species. Reforestation and regenerating projects, increase of natural fence rows (linear strips of native vegetation) to connect forest patches as well as fencing of the remaining forest to avoid further forest degradation caused by cattle grazing are beneficial strategies to be implemented in the areas where these species have stable population as these actions can increase the occupancy and abundance of these species.

## **Chapter 4: Disentangling the effect of landscape change on primate species' group density, group size and composition**

(To be submitted to Biological Conservation)

### **Introduction**

Primates are one of the most threatened taxa globally (Rylands et al. 2008a; Schipper et al. 2008; Schwitzer et al. 2015). Two of the main threats for primates are habitat loss and fragmentation (Marsh et al. 2013), but there is still a lack in understanding how these processes affect the size and composition of primate groups. It is important that we understand this because group size and composition affects many aspects of social species including reproductive and developmental rates, individual stress levels, disease susceptibility and individual and group behavior (Borries et al. 2008; Majolo et al. 2008; Chapman & Valenta 2015). The long-term persistence of primate species in fragmented landscapes depends on conservation actions that incorporates considerations on group size and composition.

Primate studies about the effects of habitat loss and/or fragmentation mainly focus on changes in presence and abundance due to habitat fragment size and isolation (Harcourt & Doherty 2005; Arroyo-Rodriguez et al. 2013a; Arroyo-Rodriguez & Fahrig 2014; Benchimol & Peres 2013). However, there are multiple reports in the primate literature about group size increases or decreases and changes in composition that seem to be attributed to the effect of habitat loss and/or fragmentation (Onderdonk & Chapman 2000; Wieczkowski 2005; Arroyo-Rodriguez & Dias 2010; Boyle & Smith 2010b; Baranga et al. 2013). In particular, group size and composition influences the fitness of each individual (Van Schaik 1989; Isbell 1991; Majolo et al. 2008), affecting the proportion of females and immatures relative to males of primate species living in fragmented landscapes. Yet, there is only one study that aims to quantify this by correlating landscape



attributes to changes in group size and composition focusing on black howler monkeys (*Alouatta pigra*) (Arroyo-Rodriguez et al. 2013b). This study found that both patch-scale and landscape-scale metrics affect black howler monkey populations. Nonetheless, there is a lack in a proper understanding of how habitat variables affect group size and composition of primate species and this understanding could be critical for enhancing species' persistence in fragmented landscapes.

Living in groups is common in vertebrates, with primates being one of the most studied taxa (Mann et al. 2000; Isbell & Young 2002; Majolo et al. 2008; Ebensperger et al. 2012). In primates, group size can be small or large depending on the species and local ecological and social conditions (Isbell & Young 2002). Group size, composition and individual dispersal determine and limit the number of options available for individuals, all of them a consequence of ecological adaptation and habitat specificity (Dunbar 1996). Optimal group size and its variations are the result of a series of individual responses made by animals in a given habitat and these are influenced by environmental conditions (Dunbar 1996; Majolo et al. 2008; Ebensperger et al. 2012). The balance between cost and benefits associated with group size differences influences the behavior and fitness of group members (Van Schaik 1989; Isbell 1991; Majolo et al. 2008). Some of the factors associated with the costs and benefits of living in groups are: competition for food, risk of predation, energetic cost of moving, access to mates and conservation of heat and water (Krause & Ruxton 2002; Chapman & Pavelka 2005; Majolo et al. 2008).

In fragmented landscapes, a reduction in the amount of habitat will reduce the resources available to primate groups (Cordeiro & Howe 2001; Worman & Chapman 2006). This reduction in resources can increase competition between individuals and groups and may determine the upper limit of group size (Terborgh & Janson 1986; Wrangham et al. 1993; Chapman & Pavelka 2005; Gogarten et al. 2015). For example, in larger groups, access to food sources and defense is easier than in smaller groups, therefore larger groups will experience less between-group

competition for food (contest competition; Janson & Van Schaik 1988; Chapman & Pavelka 2005; Chapman & Valenta 2015). In addition, larger groups may experience less predation because vigilance and defense from predation are expected to be more efficient (Janson & Van Schaik 1988; Grove 2012). However, the cost for these large groups is more within-group competition for food (contest and scramble competition; Janson & Van Schaik 1988; Isbell 1991; Chapman & Valenta 2015). Therefore, group size changes have been suggested as one of the cascading impacts of human disturbance (Chapman & Valenta 2015).

The relationships between females, how strong the bonds between females are, and how related they are, are important factors shaping the social structure of primate species (Chapman & Rothman 2009). This social structure influences the mating, parental decisions and fertility rates in primate species (Van Schaik 1989; Dunbar 1996). In particular, group composition in primates is mainly determined by the influence that resource abundance and distribution have on shaping relationships between females (Wrangham 1980; Isbell & Young 2002; Koenig 2002). Relationships between females determine to a large degree the group composition because it has an influence in the number of males associated with groups of females (Isbell & Young 2002; Koenig 2002). In fragmented landscapes primate species groups face additional challenges as resource abundance and distribution are affected by the effects of habitat loss and fragmentation on plants (Laurence et al. 2011). These effects change the relationships between males and females due to between-individual competition, affecting the sex-ratio found in primate groups, and therefore the individual reproduction strategies.

In this paper I determine the relative importance of selected site, patch and landscape scale variables on group density, group size and composition of four primate species in the Colombian Llanos, using a Bayesian state-space model. I found that group densities are primarily driven by landscape variables for most species, while group size is influenced primarily by site-scale variables. Group composition for all primate species studied here (*Alouatta seniculus*, *Callicebus*

*ornatus*, *Sapajus apella fatuellus* and *Saimiri cassiquiarensis albigena*) was largely only influenced by group size.

## Methods

### Study Area

This study was conducted in the Colombian Orinoquia, in the Llanos bioregion (sensu Lasso et al. 2010) near the town of San Martin (Figure 7a, Chapter 3). The Llanos bioregion is characterized by rivers originating in the Andes and running east as part of the Orinoco River drainage system. The region is located on lowland alluvial terraces and plains (Lasso et al. 2010). The region's vegetation is classified as savannah, gallery forest associated with water courses and lowland forest (usually gallery forest) (Lasso et al. 2010). Five primate species live sympatrically in this region: red howler monkey (*A. seniculus*), dusky titi monkey (*C. ornatus*), black-capped capuchin (*S. apella*), Colombian squirrel monkey (*S.c. albigena*) and Brumback's night monkey (*A. brumbacki*) (Carretero-Pinzón 2013a). This study focuses on the first four primate species present in this bioregion, all with diurnal habits.

### Survey Design

**Site selection:** Ninety forest fragments in the piedmont of the Orinoquia region were selected (Figure 7b, Chapter 3). A randomly stratified survey design (Rogerson 2010) based on forest fragment size and the percentage of forest surrounding each patch at a 1000 m buffer distance were used to select potential sites for primate and vegetation surveys. This was based on a land cover map derived from a mosaic of Landsat 7 ETM images from 2000 ([www.earthexplorer.usgs.gov](http://www.earthexplorer.usgs.gov)) at a 30 m spatial resolution using a supervised classification with ArcMap 10.1 (ESRI ArcGIS 10), as in Chapter 3. A combination of proportion of forest cover surrounding the fragments and forest fragment size (9

classes, Table 5, Chapter 3) was used to randomly select 10 sites per habitat class with sites widely distributed across the study area. Chosen fragments were separated by at least 1 km to minimise spatial autocorrelation among fragments.

Permission for data collection in the randomly selected sampling sites was obtained from landowners. Selected sites located more than 60 km from the focal area of San Martin, that were near areas of social conflict (guerrillas), were eliminated due to logistical and security constraints. Eliminated sites were replaced with alternative sites, using the same criteria for selection (combinations of proportion of forest around each fragment and fragment size) used previously. A minimum canopy height of the final set of selected fragments was evaluated in the field. Fragments with canopies less than 10 m in height were classified as regeneration or regrowth forest and were not included in the study because I only aimed to survey primary forest. Forest fragments wrongly classified that were palm oil plantations were eliminated. A total of 81 fragments were surveyed.

### **Primate surveys**

One km transect was located randomly in each fragment, with transect direction randomly chosen. Where possible transects were straight, but in fragments with irregular shapes the direction was varied according to fragment form. Each fragment was surveyed at least three times. The greatest effort was made in the largest fragment (1080 ha) to compensate for its size (three transects with a minimum of six km walked for each transect). Count data were collected by registering every group and individual of each species observed during the transect surveys. Each transect was walked at approximately 0.5 km/h. A minimum of 15 minutes was taken, when a primate group was visually detected, to count the group members and determine group composition (number of males, females and immatures), and the time of detection was registered. Additionally, I noted if the observed group was composed of only one individual (solitary group type), only males (bachelor group type, typical of Colombian squirrel monkeys) or groups composed of males, females and immature individuals (reproductive group type).

The coordinates of each group observation were registered using a GPS. Counts were performed during diurnal transect surveys, from 0600 to 1100 and again at 1330 to 1630 in the same day or on consecutive days. Only diurnal primate species were surveyed. In heavy rain no surveys were conducted. All observations and species identification were aided by binoculars, and primate species classification followed Defler (2010), Mittermeier et al. (2013), and Ruiz-Garcia & Castillo (in press).

### **Vegetation surveys**

I located four 10 x 50 m plots every 250 m along each 1 km transect, for vegetation surveys. For each plot, all trees with a diameter at breast height (DBH) >10 cm were identified to species level and measured. In the same plots, the presence of trees with flowers, young leaves and fruit were also registered. The number of stumps cut by humans and their respective DBHs were registered in each plot. Species identification was based on reproductive and vegetative material using the guide “Guía de frutos de La Macarena” (Stevenson et al. 1998) as well as expert identification by Francisco Castro (Botanist of Los Llanos University), a specialist in the local trees. Presence of natural fence rows (defined as tree-lines used to divide adjoining pastures, Carretero-Pinzón et al. 2010) and a classification of the surrounding matrix were made by direct observation for each fragment. The landscape matrix surrounding the forest fragments was based on the following categories: pastures (including introduced pastures or natural savannahs) and plantations (crops and palm oil plantations). In addition, canopy height and the percentage of canopy cover were registered every 200 m along the transect. Primate and vegetation surveys were conducted mainly by the first author alone or with the trees specialist Francisco Castro.

### **Variable selection**

Based on the primate literature and the variables used by Carretero-Pinzón et al. (in review, Chapter 3), a combination of selected ecologically-relevant site-scale, patch-scale and landscape-scale variables was chosen (Table 8). I selected

variables that meet one or both of the following criteria. First, they were previously suggested as habitat variables influencing the primate group sizes such as measures of resource availability or could influence individuals' ability to move between forest patches (matrix type and presence of natural fence rows). Second, they were found to have a high influence on the studied primate species occupancy and abundance (Carretero-Pinzón et al. in review, chapter 3). The variables selected were: at the site-scale number of food trees, number of trees with fruits, and canopy height; at the patch-scale matrix type, presence of natural fence rows, and fragment size; and at the landscape-scale percentage of forest cover. All pairs of variables had Spearman's rank correlation coefficients of less than 0.7 so levels of collinearity were deemed acceptable. The landscape variable, percentage of forest cover, was measured at a buffer radius distance of 1000 m, which was the spatial landscape extent most important for most of the species studied (dusky titi monkeys, black-capped capuchins and Colombian squirrel monkeys) (Carretero-Pinzón et al. in review, chapter 3). The map with selected fragments was further corrected using a forest and non-forest map of Colombia produced by IDEAM (2014) that is based on satellite images from 2010, for more precision on land cover classification and fragment sizes.

**Table 8 Summary of site, patch and landscape variables selected from previous models as predictive variables of primate group size and composition.**

<b>Variable Name</b>	<b>Description</b>	<b>Reference</b>
<b>Landscape Scale</b>		
Percentage of forest cover	Percentage of forest present within each buffer (only 1000 m)	Arroyo-Rodriguez et al. 2013b
<b>Patch Scale</b>		
Patch size	Size in hectares of each fragment surveyed	Arroyo–Rodriguez et al. 2013b
Matrix type	Presence of crops, African palm oil plantations and pastures surrounding the focal fragment. Only two categories were used for the analysis: pastures (includes natural savannahs and small crops) and African palm oil plantations	Anderson et al. 2007b, Blair & Melnick 2012
Presence of living fences	Presence of living fences	Carretero-Pinzón et al. 2009, 2010
<b>Site Scale</b>		
Average Canopy Height	Canopy height measure taken with a digital rangefinder every 200 m in each transect	Pozo-Montuy et al. 2008, Anzures-Dadda & Mason 2007
Number of food plants consumed by primate species by transect	Number of all plant species consumed by each primate species found in all strips in each transect	Chapman et al. 2006b <sup>1</sup>
Presence of trees with fruits	Number of trees with fruits, flowers or young leaves present at the moment of the vegetation surveys, in all strips in each transect	Chapman & Onderdonk 1998

<sup>1</sup>The list of plant species consumed by each primate species studied here was based on the following references by primate species: *Alouatta seniculus*: Escudero 2005, Beltran 2005, Santamaria 2005, Ramos 2007; *Sapajus apella*: Torres 2005, Ramos 2007, Gómez-Posada 2012a, 2012b, Fragaszy et al. 2004; *Saimiri cassiquiarensis albigena*: Carretero-Pinzón 2000, 2008; *Calliebus ornatus*: Ospina 2006.

I modelled the number of groups, group size and group composition as functions of the site-scale variables, patch-scale variables and 1000 m buffer landscape scale variable. I formulated several hypotheses based on the information theoretic approach (Burnham & Anderson 2002). I hypothesized that the number of groups, group size and composition of each primate species were determined by one of the following variables: 1) number of food trees (site-scale variable), 2) number of trees with fruits (site-scale variable), 3) canopy height (site-scale variable), 4) fragment size (patch-scale variable), 5) matrix type (patch-scale variable), 6) natural fence rows (patch-scale variable), and 7) percentage of forest cover (landscape-scale variable). In addition, I calculate the relative importance of each variable included against each other. I constructed all models using JAGS (<http://mcmc-jags.sourceforge.net>) and fitted the models to the data using Markov Chain Monte Carlo (MCMC) in JAGS (<http://mcmc-jags.sourceforge.net/>) using the “runjags” package in R (<http://www.r-project.org/>). I simulated three MCMC chains using overdispersed starting values and a burn-in of 20,000 iterations and then retained 20,000 iterations per chain. Convergence was assessed using the Gelman and Rubin convergence statistic (R-hat) (Gelman & Rubin 1992). See Appendix E for the JAGS code.

## **Statistical Analysis**

I used a Bayesian state-space model to characterize the effect of the habitat variables on primate species group numbers (density), group size and composition. Group density in this case is related to population density because more groups in an area means a higher population density, all other things being equal. A Bayesian state-space model is defined as a hierarchical model that explicitly



models the underlying ecological or “state” process and the data observation processes with parameters estimated within a Bayesian framework (Kéry & Schaub 2011). The advantages of this framework include the explicit representation of detection error and the ability explicit represent prior information about the model (Kéry & Schaub 2011). I modelled the number of groups using an N-mixture model following Royle (2004). I assumed that the true number of groups at each site (transect) was described by a Poisson distribution such that

$$G_i \sim \text{Poisson}(\lambda_i),$$

where  $G_i$  is the number of groups using site  $i$ ,  $\sim$  means “distributed as”, and  $\lambda_i$  is a function of covariates where

$$\log(\lambda_i) = \boldsymbol{\alpha}^T \mathbf{X}_i, \quad \text{Equation 1}$$

where  $\boldsymbol{\alpha}$  is a vector of coefficients and  $\mathbf{X}_i$  is a vector of covariates for site  $i$ . Since groups are never be detected perfectly, detection error is introduced by assuming that the actual number of groups observed is less than the true number of groups such that

$$N_{i,j} \sim \text{Binomial}(p, G_i),$$

where  $N_{i,j}$  is the number of groups observed at site  $i$  during repeat survey  $j$  and  $p$  is the probability of detecting a group given that it uses a site (i.e., detection probability). Note here that because primates are highly mobile, it is unlikely that each transect is strictly closed between repeat surveys (an assumption of the N-mixture model, Royle 2004) even though repeat surveys occurred temporally close together. Therefore, the detection probability estimate is likely to confound errors arising from groups that were present at the time of the survey but not observed with groups that used the transect but were not present at the time of the survey (Martin et al. 2005). Consequently, we interpret  $G_i$  as the true number of groups

using the transect over the survey period rather than the number of groups present during a single survey.  $G_i$  therefore represents an index of relative density rather than an unbiased estimator of actual density (Mackenzie et al. 2002).

For group size I assumed that group size followed a zero-truncated Poisson distribution (Zuur et al. 2009) so that

$$S_i \sim \text{ZTPoisson}(\mu_i),$$

where  $S_i$  is the size of group  $i$ , ZTPoisson is the zero-truncated Poisson distribution, and  $\mu_i$  is a function of covariates so that

$$\log(\mu_i) = \beta^T \mathbf{Y}_i, \quad \text{Equation 2}$$

where  $\beta$  is a vector of coefficients and  $\mathbf{Y}_i$  is a vector of covariates for group  $i$ .

For composition I assumed that the number of males, females, immatures and unknowns follows a multinomial distribution so that

$$\mathbf{C}_i \sim \text{Multinomial}(\mathbf{q}_i, S_i),$$

where  $\mathbf{C}_i$  is a vector of the number of males, females, immatures, and unknowns in group  $i$ , and  $\mathbf{q}_i$  is a vector of the probabilities that each individual is a male, female, immature or unknown in group  $i$ . Then to ensure that entries in the vector  $\mathbf{q}_i$  sum to one I set

$$q_{ij} = \frac{\phi_{ij}}{\sum_{j=1}^4 \phi_{ij}} \quad \text{Equation 3}$$

where  $q_{ij}$  is entry  $j$  in the vector  $q_i$  and  $\phi_{ij}$  is a function of covariates such that

$$\log(\phi_{i1}) = 0$$

$$\log(\phi_{i2}) = \gamma_1^T \mathbf{Z}_i$$

$$\log(\phi_{i3}) = \gamma_2^T \mathbf{Z}_i$$

$$\log(\phi_{i4}) = c$$

where  $g_1$  is a vector of coefficients for the probability of a female and  $g_2$  is a vector of coefficients for the probability of an immature,  $\mathbf{Z}_i$  is a vector of covariates for group  $i$ , and  $c$  is a parameter that determines the probability of an unknown. Note that because I set  $\log(\phi_{i1}) = 0$  the effects of covariates on probabilities of a female, immature or unknown are relative to the probability of a male. Finally, this formulation assumes that the probability of an unknown does not depend on any covariates because this is part of the observation process alone.

Model or variable selection for Bayesian models is often conducted using Bayes Factors or Deviance Information Criteria (Kass & Raftery 1995; Ellison 2004). However, for complex state-space models with missing data this, can be problematic due to difficulties in calculating Bayes Factors and due to the strongly hierarchical nature of the models complicating the interpretation of Deviance Information Criteria (Celeux et al. 2006). An alternative is to use Bayesian variable selection methods where the probabilities of variable selection are explicitly incorporated as parameters in the model (O'Hara & Sillanpää 2009). These methods are easily implemented for state-space models fitted via Markov Chain Monte Carlo (MCMC) and therefore I used this approach to quantify the importance of each predictor variable via the selection probability of each variable. Using the approach of Kuo & Mallick (1998) I set

$$\boldsymbol{\alpha} = \boldsymbol{\theta}_\alpha \otimes \boldsymbol{\alpha}^*$$

$$\boldsymbol{\beta} = \boldsymbol{\theta}_\beta \otimes \boldsymbol{\beta}^*$$

$$\boldsymbol{\gamma}_1 = \boldsymbol{\theta}_{\gamma_1} \otimes \boldsymbol{\gamma}_1^*$$

$$\boldsymbol{\gamma}_2 = \boldsymbol{\theta}_{\gamma_2} \otimes \boldsymbol{\gamma}_2^*$$

where  $\boldsymbol{\theta}_\alpha, \boldsymbol{\theta}_\beta, \boldsymbol{\theta}_{\gamma_1}, \boldsymbol{\theta}_{\gamma_2}$  are vectors with binary parameters corresponding to whether a variable is included in the model or not (1 = included, 0 = not included), and  $\boldsymbol{\alpha}^*, \boldsymbol{\beta}^*, \boldsymbol{\gamma}_1^*, \boldsymbol{\gamma}_2^*$  are vectors of coefficients. For each entry,  $i$ , these parameters are assumed distributed as follows

$$\theta_{\alpha,i} \sim \text{Bernoulli}(s_\alpha)$$

$$\theta_{\beta,i} \sim \text{Bernoulli}(s_\beta)$$

$$\theta_{\gamma_1,i} \sim \text{Bernoulli}(s_{\gamma_1})$$

$$\theta_{\gamma_2,i} \sim \text{Bernoulli}(s_{\gamma_2})$$

for  $i \geq 2$  (I assumed that when  $i = 1$  [i.e., the intercept] the variable was always included in the model) and

$$\alpha_i^* \sim \text{Normal}(0, \tau_\alpha)$$

$$\beta_i^* \sim \text{Normal}(0, \tau_\beta)$$

$$\gamma_{1,i}^* \sim \text{Normal}(0, \tau_{\gamma_1})$$

$$\gamma_{2,i}^* \sim \text{Normal}(0, \tau_{\gamma_2})$$

In this formulation, the expected values for the  $\boldsymbol{\theta}_\alpha, \boldsymbol{\theta}_\beta, \boldsymbol{\theta}_{\gamma_1}, \boldsymbol{\theta}_{\gamma_2}$  vectors (the variable inclusion/non-inclusion parameters) represent the variable selection probabilities and therefore represent the level of support for each variable from the data. I interpret these as measures of variable importance (sensu Burnham & Anderson 2002) and considered variables with selection probabilities above 0.5 to be important variables.

Finally, I assumed the following largely uninformative priors

$$s_{\alpha} \sim \text{Beta}(2,8)$$

$$s_{\beta} \sim \text{Beta}(2,8)$$

$$s_{\gamma_1} \sim \text{Beta}(2,8)$$

$$s_{\gamma_2} \sim \text{Beta}(2,8)$$

$$\tau_{\alpha} \sim \text{Gamma}(1,0.001)$$

$$\tau_{\beta} \sim \text{Gamma}(1,0.001)$$

$$\tau_{\gamma_1} \sim \text{Gamma}(1,0.001)$$

$$\tau_{\gamma_2} \sim \text{Gamma}(1,0.001)$$

$$c \sim \text{Normal}(0,0.001)$$

$$p \sim \text{Uniform}(0,1)$$

where  $\alpha_i$  is entry  $i$  in the vector  $\alpha$ ,  $\beta_i$  is entry  $i$  in the vector  $\beta$ ,  $\gamma_{2i}$  is entry  $i$  in the vector  $\gamma_2$ , and  $\gamma_{3i}$  is entry  $i$  in the vector  $\gamma_3$ .

## Results

### Primate population structure for the study area

A total of 86 groups of dusky titi monkeys, 109 groups of Colombian squirrel monkeys, 151 groups of howler monkeys and 174 groups of black-capped capuchin monkeys were counted in the whole study area. Solitary individuals and reproductive groups were observed for all species and bachelor groups (groups of only adult males) were observed for Colombian squirrel monkeys.

### Variable Selection Probabilities

The variable selection probabilities (variables with the highest selection frequencies) showed that the percentage of forest cover (landscape-scale variable) is the most important variable determining the number of groups for red howler monkeys (*A. seniculus*), dusky titi monkeys (*C. ornatus*) and the Colombian squirrel monkey (*S.c. albigena*), followed closely by canopy height and number of food trees (site-scale variables) for red howler monkeys. For black-capped

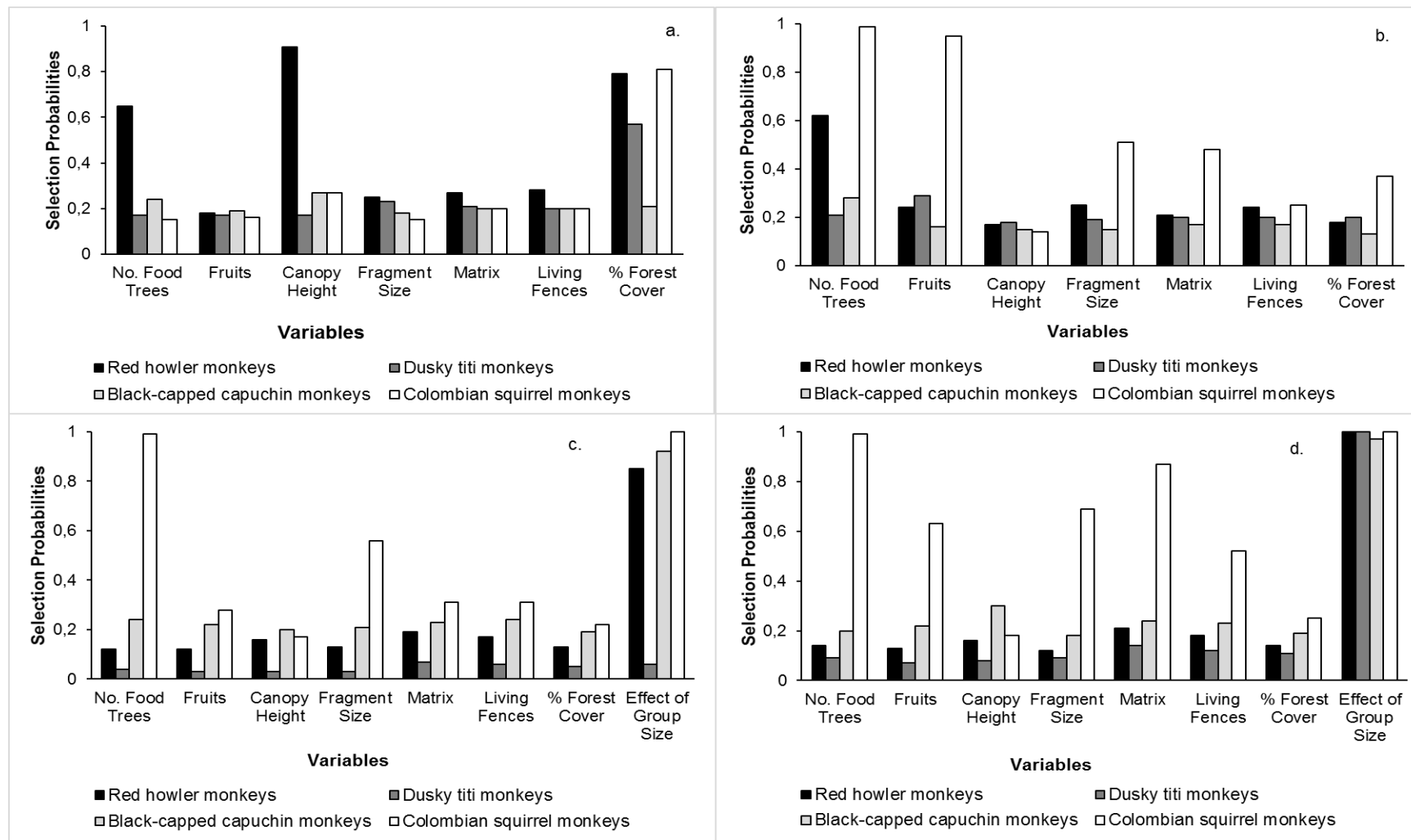
capuchin monkeys (*S. apella fatuellus*) no variables seem to be important (Figure 10a). On the other hand, group size was associated with variables measuring the resource availability at the site-scale (number of food trees and number of trees with fruits) in the Colombian squirrel monkey and red howler monkey (only number of food trees, Figure 10b). For dusky titi monkeys and black-capped capuchin monkeys none of the variables seem to be important (Figure 10b). In addition, group size in the Colombian squirrel monkeys was also associated with patch-scale variables (matrix type and fragment size). Finally, group size, and therefore indirectly site- and patch-scale variables, are the most important variables associated with the proportion of females relative to males (Figure 10c) for all primate species studied except for the dusky titi monkey, for which no clear patterns were found (Figure 10c). In the case of the Colombian squirrel monkey, a site-scale variable (number of food trees) and a patch-scale variable (fragment size) were also associated with the proportion of females relative to males. Group size was also the most important variable determining the proportion of immatures relative to males for all primate species studied. The proportion of immatures relative to males also showed important associations with site-scale variables (number of food trees and number of trees with fruits) and patch-scale variables (matrix type, natural fence rows and fragment size) for the Colombian squirrel monkeys.

### **Variable Effect Sizes**

I found a lot of uncertainty in the effect size estimates of the variables used in my model as indicated by the wide credible intervals (Figure 11). However, some variables seem to be more associated than others with the number of groups, group size and proportion of females and immatures relative to males, as described next. I found that the amount of forest around patches (landscape-scale) was negatively associated with the number of groups per transect for three primate species studied: red howler monkeys, dusky titi monkeys and the Colombian squirrel monkey (Figure 11a). The exception was the black-capped capuchin monkey for which the amount of forest around patches was not associated with the number of

groups observed (Figure 11a). A positive association with site-scale variables (canopy height and number of food trees) on the number of groups observed was found for red howler monkeys (Figure 11a). In addition, a negative association with a patch-scale variable (matrix type) on the number of groups observed was found for dusky titi monkeys (Figure 11a). The group size of red howler monkeys was negatively associated with a site-scale variable (number of food trees), while another site-scale variable (number of trees with fruits) was slightly positive associated with the group size of dusky titi monkeys (Figure 11b). Group size of the Colombian squirrel monkey was positively associated mainly with two site-scale variables, number of food trees and number of trees with fruits. In addition, Colombian squirrel monkeys group sizes were slightly positive associated with patch-scale (matrix type and fragment size) variables, while the landscape variable (percentage of forest cover) slightly constrained the group size for this species in a negative way (Figure 11b). Group size of black-capped capuchins were not associated with any of the variables used in our models.

On the other hand, group composition in terms of the proportion of females relative to males was positively associated with group size for black-capped capuchin monkeys, and slightly less for red howler monkeys, and Colombian squirrel monkeys (Figure 11c). The proportion of females relative to males for the monogamous dusky titi monkeys was not influenced by any of the variables used in this study. Additionally, the proportion of females relative to males for Colombian squirrel monkeys was also negatively influenced by a site-scale variable (number of food trees present in the transect; Figure 11c). The proportion of immatures relative to males was positively influenced by group size for all primate species studied (Figure 11d), although only with high values for dusky titi monkeys. Colombian squirrel monkeys' proportion of immatures relative to males was slightly associated positively with a patch-scale variable (matrix type) and negatively associated with a site-scale variable (number of food trees; Figure 11d).

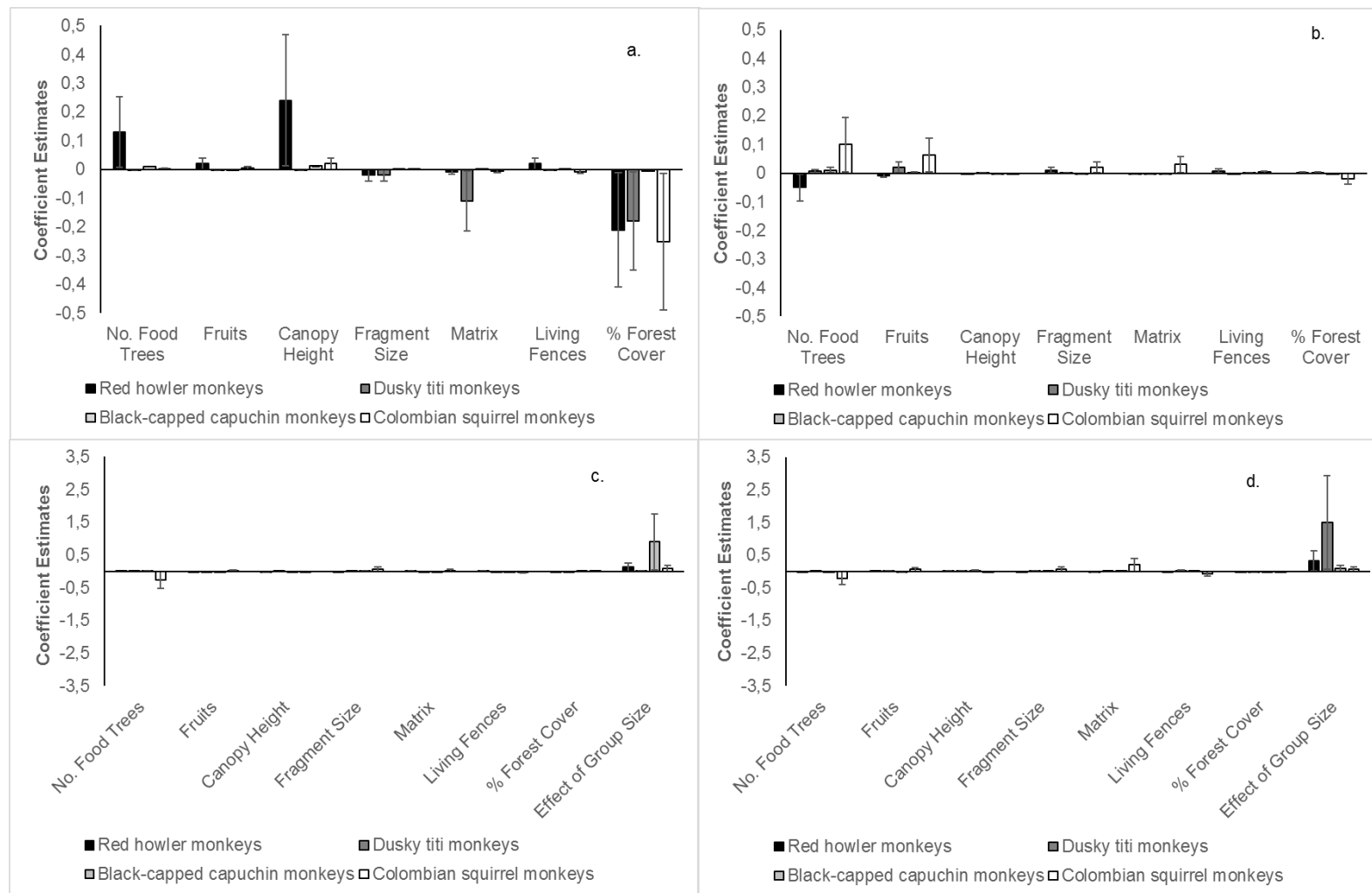


**Figure 10 Selection probabilities for: a. Number of groups observed (index of relative density); b. Group size; c. Proportion of females and d. Proportion of immatures relative to males for the four primate species studied.**



## **Discussion**

This study determined the relative importance of site, patch and landscape scale variables on group density, group size and composition of four primate species in the Colombian Llanos. This study has two main contributions. First, the density of groups found in fragments was associated primarily with landscape composition. Second, and in contrast, group size is associated with site-scale variables related to the availability of food resources found in fragments, as well as patch-scale variables that describe the context of the fragments in which these species are present. Third, the composition of primate species groups was indirectly associated with the site/ patch-scale variables through group size. Therefore, management actions implemented in fragmented landscapes that are focused on the amount of forest in the landscape will affect group density of primates on those landscapes. Whilst, if changes in group size and composition are the objective of the management actions then these management actions need to be focused on increasing resource availability, for example by planting food trees important for those primate species. The focus you chose for these management actions will depend of what is more important to reduce the effects of extinction risk.



**Figure 11 Coefficient estimates for: a. Number of groups observed (index of relative density); b. Group size; c. Proportion of females and d. Proportion of immatures relative to males for the four primate species studied.**

The importance of the amount of forest around patches (landscape composition) on group density for most of the species studied highlights one important concept in landscape ecology, the context, i.e. the matrix matter (Wiens 2009). Some previous studies of primates living in fragmented landscapes have shown that primate species use and in some cases include the matrix as part of their home ranges (Anderson et al. 2007; Boyle & Smith 2010a). These studies highlight the importance that other types of habitat such as mangrove forest, plantations and secondary forest present in the matrix have on primate species living in fragmented landscapes. Similarly, I found that landscapes with low forest cover had a greater density of groups than landscapes with high forest cover for at least three of the primate species studied. Highly fragmented landscapes are expected to contain a high number of fragments, a reduction in the mean size of those fragments and an increase in mean fragment isolation distance (Fahrig 2003). This landscape pattern can reduce the dispersal opportunities of individuals and result in crowding effects for some species. Crowding effects can also be explained as a consequence of competition release due to local extinction of other competitive species (McArthur et al. 1972). Some studies have reported crowded primate populations in small fragments with high isolation (Gillespie & Chapman 2008; Wagner et al. 2009; Carretero-Pinzón 2013a), although none of these studies have tried to explain how landscape variables are associated with those higher densities.

One of the challenges faced by primate species in fragmented landscapes is changes in food resource abundance and distribution due to the effects of habitat loss and fragmentation on plants (Laurence et al. 2011). My study explicitly tests the effect of food resource abundance at the site-scale on group size for primate species, highlighting the importance that site-scale variables such as number of food trees and number of trees with fruits have when compared with landscape-scale or even patch-scale variables. Competition between and within groups is affected by those changes in food resource abundance that determines the cost and benefits of group sizes (Chapman & Pavelka 2005; Chapman & Valenta 2015; Gogarten et al. 2015). In addition, it is interesting that group size did not show a high dependence on fragment size, since it is generally assumed that larger fragments can support larger group sizes, if not constrained by ecological and behavioral characteristics of the species (Boyle & Smith 2010b). Some studies have shown that primate species

groups in small fragments tend to be smaller than groups of the same species in continuous areas (Chapman et al. 2007; Carretero-Pinzón 2013a, b). However, it is not the fragment size which seems to drive those changes on group size in my study system but food abundance.

Further, changes in food resource abundance at the site scale have an indirect influence on group composition through its association with group size. Food resource abundance and distribution seem to be the main factor shaping the social relationships established between females in primates (Wrangham 1980; Isbell & Young 2002; Koenig 2002). Female relationships (how related they are and how strong their bonds are) influence to a great extent the size and composition of primate groups due to their role in determining the number of males associated with groups of females (Isbell & Young 2002; Koenig 2002). My results highlight the strong effect that group size, and therefore, indirectly site-scale variables, has on the proportion of females and immatures relative to males found in each group. It is important to understand this influence as the group composition has a large influence on the fertility rates and mating systems of primate species (Van Schaik 1989; Dunbar 1996), and therefore needs to be considered when managing primate populations in fragmented landscapes.

This study provides insights into the mechanisms by which different scales influence primate species. Landscape scale affects group density whereas site and patch scale affects within group dynamics. This has only partially highlighted in previous studies of black howler monkeys (Arroyo-Rodriguez et al. 2013b), but not using multiple species. Therefore, my study give specific guide of how changes at multiple scales are affecting primate groups dynamics as well as how general are those effects across different species in the same community.

### **Limitations of this study**

An important limitation of our modelling approach is the closure assumption in the N-mixture model used to account for the detectability of groups (Royle 2004). This refers to the assumption that the survey sites are closed (i.e. no emigration or immigration, temporal o permanent) during the period over which the repeat surveys at each site are conducted (Rota et al. 2012). One way to avoid violation of the

closure assumption is to minimize the time between surveys (Mackenzie et al. 2006; Rota et al. 2012), and that was the strategy used in this study. However, primates are mobile animals that can use large areas as part of their home ranges. These home ranges vary in size depending on the species and are used in a seasonal pattern depending on the availability of the food resources important for the studied species (Fleagle 1999; Defler 2010). The species studied in this thesis have a variety of home ranges sizes ranging from a few hectares to several hundreds of hectares and usually with a high overlapping between home ranges of neighboring groups (Defler 2010; Ospina 2006; Carretero-Pinzón 2008). Therefore, the movement of groups within their home ranges may mean that the closure assumption may be violated even though repeat surveys were conducted in quick succession of one another. The implications of this is that estimates of group density may be biased. Nonetheless it is likely that group densities will be robust if treated as relative group densities.

### **Conservation Implications**

This study has shown that changes in the amount of forest at the landscape scale affects the density of groups but is much less important for the sizes and composition of those groups. Group size and composition depend on site-scale variables related to food resource availability. So if the purpose of conservation action is to decrease the abundance of primate species (i.e. group density) in a fragmented area the management need to be directed towards an increase in the amount of forest around patches where the species is present. This is particularly true for at least three of the species in this study, red howler monkeys, dusky titi monkeys and the Colombian squirrel monkeys. But if the purpose of the conservation actions is to change group size and indirectly change group composition then the management actions mainly need to be focus on increasing the food resource availability (number of food trees, especially the ones important for its fruits) for all species but mainly for red howler monkeys and the Colombian squirrel monkeys. Interestingly, for the Colombian squirrel monkeys group size and composition are not only affected by site-scale but also patch-scale variables, therefore for this particular species, conservation actions that aims to manage group size and composition have to involve not only improvements on food resource

availability but also fragment size and the context in which those patches are immersed (type of matrix and presence of natural fence rows). The Colombian squirrel monkeys are the only primate species in my study area that typically have group sizes above 20 individuals, in which the proportion of females and immatures is higher compared with the proportion of males (Carretero-Pinzón 2000, 2008, Defler 2010). Therefore, for this endemic species, conservation actions towards increasing their group density, with considerations of their group size and composition need to involve actions at all scales. For the other endemic species in my study area, the monogamous dusky titi monkeys, conservation actions towards decreasing their groups density need to consider the amount of forest around patches. But if the conservation objective is to increase the proportion of immatures relative to males (or in this case also relative to females), conservation actions need to involve improvement on food resource availability in forest patches inhabited by groups of this species.

From a conservation perspective, management actions that lead to changes in group size and composition, as suggested before, also need to consider the implications that those changes can have in the demography of the species. For example, in a fragmented landscape where a species shows variation in group size and composition, these differences can influence the individual fitness of each animal depending on the size of the group (Van Schaik 1989; Isbell 1991; Majolo et al. 2008). In addition, the sex ratios (proportion of females:immatures and males:females in each group) can also be affected, influencing reproduction rates (Van Schaik 1989; Dunbar 1996) and subsequently the infants survivorship (i.e. increase infanticide events due to a high turnover of male dominance, Crockett 1996). These considerations would need to be evaluated for each species before implementing any management action that will lead to modifications of group size and composition.

My study contributes to understand the implications of management actions at different scales for primate conservation in fragmented landscapes. This is particularly important for the endemic species present in my study area, dusky titi monkeys and Colombian squirrel monkeys, which are both threatened by landscape change. My approach to the study of the effects that landscape change produce in

group densities and group dynamics can be used for primate conservation of other Neotropical species.

## **Chapter 5: Prioritising conservation areas for primates in fragmented landscapes**

(To be submitted to PLoS ONE)

### **Introduction**

At least 50 % of primate species are threatened globally (Rylands et al. 2008a; Schipper et al. 2013; Schwitzer et al. 2015). These primate species live in fragmented landscapes composed of agriculture, forest patches and human settlements. The spatial configuration and composition of these landscapes have important influences on the spatial distribution and persistence of primate species (Arroyo-Rodriguez et al. 2008; 2013b). However, only until recently has there been an incorporation of landscape level planning and systematic conservation planning for primate conservation. This approach has been used to prioritise conservation areas for endangered primate species in a region with high human population using occurrence data (Plaza-Pinto & Viveiros-Grelle 2009; Plaza-Pinto & Viveiros-Grelle 2011) and distribution data (Carlsen et al. 2012). However, none of these studies have used spatial models of species abundance to prioritise conservation areas for primate conservation in highly fragmented areas.

The majority of conservation plans focused on primate species, particularly apes, has been developed under the guideline of the IUCN Primate Specialist Group with the involvement of government agencies, primate experts and conservation NGO's to evaluate and propose conservation actions at the national or regional scale (IUCN/ SSC Primate Specialist Group 2015). Primate conservation action plans have also been done by government agencies of primate habitat countries to select areas and identified threats for primate species at the national level (ICMBio 2015). These primate conservation action plans have been focused on population viability, habitat modelling and threat analyses (Oates et al. 2007; Carlsen et al. 2012; Dunn et al. 2014). Recently, these action plans have modified their analytical tools to incorporate more spatially explicit analyses of threats and actions to increase protected area impacts and landscape management that involves human conflict (IUCN & ICCN



2012; Maldonado et al. 2012). Conservation planning tools have been incorporated slowly as an approach to make more informed decisions of where to focus conservation actions and efforts, especially for great apes (Carlsen et al. 2012). Other studies have incorporated systematic conservation planning concepts and methods to prioritise conservation areas for mammals and other vertebrate taxa in Africa (Cowling et al. 2003; Kerley et al. 2003; Brugiére & Kormos 2009), South America (Illoldi-Rangel et al. 2008; Loyola et al. 2009), Madagascar (Kremen et al. 2008) and Asia (Das et al. 2006). Only two studies have focused specifically on prioritizing conservation areas for primate species, both for endemic species of the Brazilian Atlantic forest (Plaza-Pinto & Viveiros-Grelle 2009; Plaza-Pinto & Viveiros-Grelle 2011). Further, although there are many primate studies that are based on the ecology and behaviour of specific species that propose the need to create reserves and conservation actions (Chapman et al. 2007; Chagas & Ferrari 2011; Peng-Fei et al. 2011), none of these have used conservation planning concepts or methods.

Systematic conservation planning is a systematic approach to identify conservation priorities to meet specific conservation objectives that focus on locating, designing and managing protected areas that represent the biodiversity of a region (Margules & Pressey 2000; Margules & Sakar 2007; Possingham et al. 2010; Veloz et al. 2015). A central point of the conservation of biological diversity is the establishment of conservation area networks, which are managed to minimize the risk of extinction and systematic conservation planning can play a role in this respect (Margules & Pressey 2000; Margules & Sakar 2007; Pressey et al. 2007). In fragmented landscapes where species co-exist with human activities, the prioritising process need to involves measures of the cost to implement and manage areas or landscapes for biodiversity conservation (Polaski et al. 2005; Bode et al. 2008; Polaski et al. 2008). The incorporation of cost in systematic conservation planning can be challenging as not always spatial explicit cost such as land acquisition price is available (Naidoo & Ricketts 2006; Armsworth 2014). Therefore, surrogates of cost have been used such as area (Stewart & Possingham 2005), human population density (Luck et al. 2004; Plaza-Pinto & Viveiros-Grelle 2011), to incorporate the socio-economic cost of stablishing or managing conservation areas (Adams et al. 2010; Cameron et al. 2010). This is particularly important in fragmented areas where conservation is in conflict with economic activities.

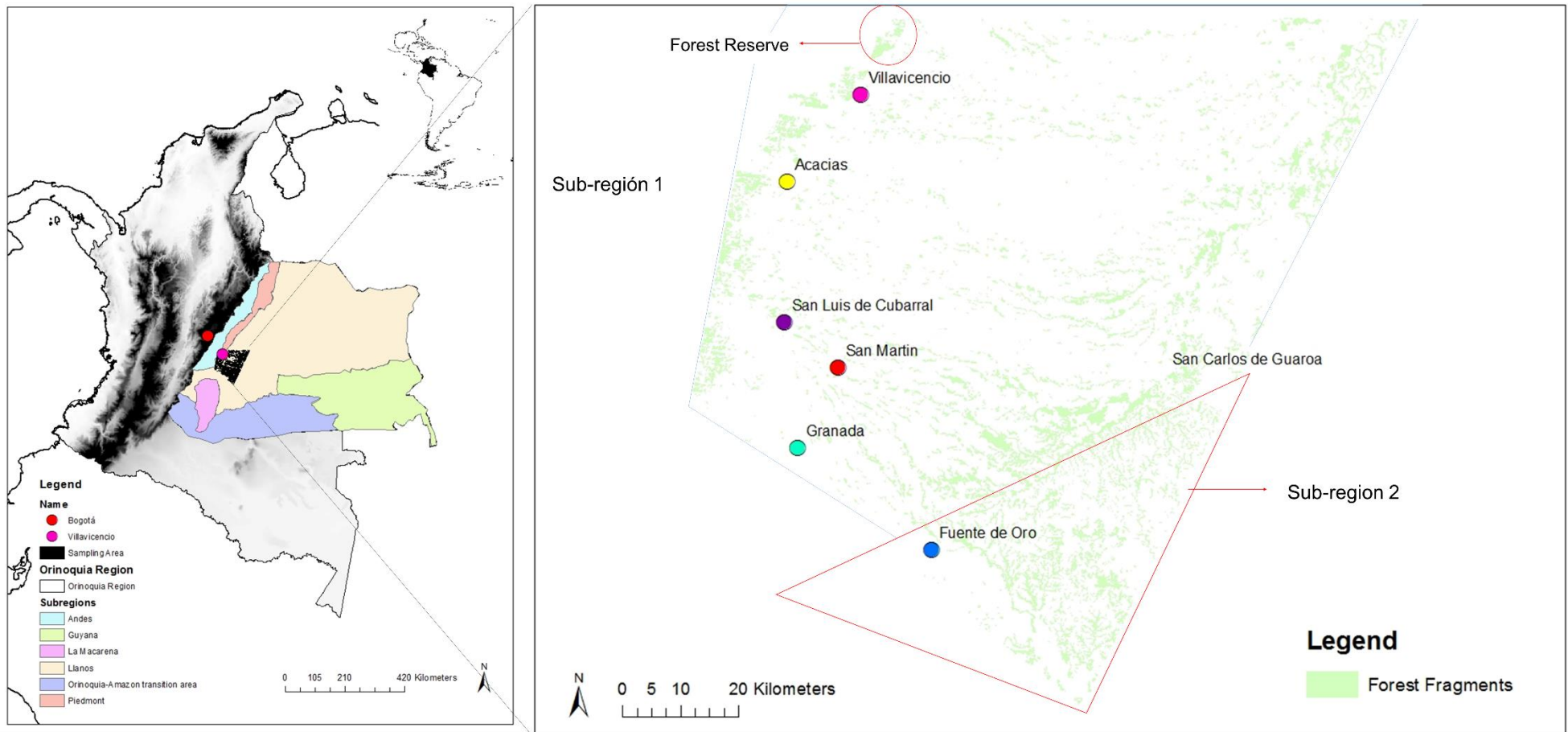
The aim of this paper is to assess conservation area priorities for primates in a highly fragmented part of the Colombian Llanos, and evaluate the shape of the trade-off between cost and primate abundance targets across alternative cost surrogates. I used the conservation planning software Marxan (v. 1.8.10) (Possingham et al. 2000), to prioritise conservation areas while meeting a representative target of primate species abundance at a minimal cost in a highly fragmented area. I found that although the shape of the relationship between cost and targets is similar for the costs analysed (i.e. area, inverse distance to nearest town and the combination of both), the conservation target was achieved at a lower relative cost by using the combination cost compared with areas and inverse distances to the nearest towns. In addition, each cost structure showed a different spatial arrangement indicating the sensitivity of conservation priority to cost assumptions. For the study region considered here, the north-east and south-east parts of the study region, that concentrate a good proportion of the selected fragments, seems to be the zones in which primate conservation need to focus.

## **Methods**

To select priority areas for primate conservation in a highly fragmented part of the Colombian Llanos, as well as to evaluate the relationship between cost and targets, I use some of the systematic conservation processes (steps 2 to 6; for detail about these step see Possingham et al. 2010). To determine priority of conservation areas for primates in this region, I developed several steps: 1) Selection of forest patches to be used in the prioritization process; 2) spatial predictions of relative abundance of primate species in forest patches; 3) calculate the cost for protecting each forest patch; and 4) identify priority conservation units to achieve different targets (range 10-90% of total current total abundance for each primate species); and 5) evaluate the relationship between the selected cost and the conservation targets. The goal of my analysis was to identify forest patches that, if selected, would be least costly to implement in a highly fragmented area of the Colombian Llanos for primate conservation and assess the trade-off between cost and conservation benefit for alternative cost assumptions.

## Study Area

This study was located in the piedmont of the Colombian Llanos between the main capital city in the region (Villavicencio) and one of the largest towns, Granada (Figure 12). The Llanos is characterized by lowland alluvial terraces and plains, dissected by rivers originating in the Andes or in the upland savannahs and draining into the Orinoco River (Lasso et al. 2010). The vegetation is dominated by flooded and dryland savannas, gallery forest associated with drainage lines and lowland rainforest (Lasso et al. 2010). There are five primate species living sympatrically in the region: red howler monkey (*Alouatta seniculus*), dusky titi monkey (*Callicebus ornatus*), black-capped capuchin (*Sapajus apella fatuellus*), Colombian squirrel monkey (*Saimiri cassiquiarensis albigena*) and Brumback's night monkey (*Aotus brumbacki*; Carretero-Pinzon 2013a). This study focuses on the four diurnal species. This study area has been a colonization and agriculture frontier since 16<sup>th</sup> century (Rauch 1994; 1999). The area is a highly and rapidly transformed area economically focused on cattle ranching; palm oil plantations and petrol exploration and exploitation continues in continuous expansion (Fedepalma 2014; Ecopetrol 2015).



**Figure 12 Study area showing the towns and forest reserves locations. Area inside of the blue lines (sub-region 1) is classifies as piedmont and the area inside of the red triangle (sub-region 2) is classified as high plateau following IGAC 2015.**

### **Defining planning units (forest patches)**

The planning units were defined as all forest patches that remains in the study area with an area greater than 4.5 ha. This area was selected as the minimum area because it was the minimum patch size in which primates were found in a previous spatial study of primate species occupancy and abundance (Carretero-Pinzón et al. in review, chapter 3). Polygons were extracted from a forest and non-forest map produced from 2010 Landsat images (IDEAM 2014). A total of 2524 planning units were used for the prioritising process. The study area defined here does not have any National Parks but it has two small forest reserves manage at the national level (Figure 12, Vásquez & Serrano 2009).

### **Abundance predictions**

Occurrence, abundance, group density, size and composition of four of the five primate species present in forest fragments in these area is available from some fragments in the southern part of the study area ( $n = 81$ ). However, predictions of relative abundance for all forest patches were generated using a Bayesian state-space model (Chapter 4; Appendix F for details of the JAG and R code for the predicted abundances). This relative abundance was calculated by first calculate the predicted density as predicted group size multiplied by predicted number of groups on a 1 km transect and then multiplied this by area (Chapter 4).

To calculate the habitat variables for all the forest patches included in this analysis of which I did not have field data, the study region was subdivided into two sections using a soils map of Colombia produced by IGAC (Mapa de Geopedologia; Figure 12). These two sub-regions differed on a combination of slope (sub-region 1:  $> 12\%$ ; sub-region 2:  $< 7\%$ ), soil type (sub-region 1: entisols and inceptisols; sub-region 2: entisols, inceptisols and oxisols, USD soil taxonomy terms) and type of drainage (sub-region 1: poor to very poor; sub-region 2: imperfect to excessive) that produce two different types of landscapes (piedmont and high plateau, respectively; IGAC 2015). Although I do not have the same or equivalent number of sampled forest patches in these two sub-regions, I average the habitat variables

used to predict the primate relative abundances for the remained forest patches present on these two sub-regions. The habitat variables used to make abundance predictions are described on Table 10. I then standardize the relative abundance of each primate species studied in each patch so that it was the proportion of the total abundance in the study area. This was done to give equal value to relative abundance for each species in the prioritisation.

The systematic conservation planning approach used for this study was based on the minimum set problem, which aim to minimize resources expended (such as areas allocated to conservation) subject to the constraints that all features meet their conservation targets (Possingham et al. 1993, Wilson et al. 2005). Due to the economic importance of the study area (i.e. for petrol exploration and exploitation and palm oil plantations), the amount of area that can be set aside for conservation purposes is limited; therefore, the minimum set problem is the appropriate approach for this region. I used the proportion of the total primate relative abundance for each species as our conservation targets.

**Table 10 Habitat variables used to model relative abundance of four primate species in the study region**

<b>Variable Name</b>	<b>Description</b>	<b>Use for generating predictive abundance</b>
<b>Landscape Scale</b>		
Percent forest cover	Percentage of forest present within a 1000 m buffer around each forest fragment	This variable was calculated for each fragment in the study area
<b>Patch Scale</b>		
Patch size	Size in hectares of each fragment surveyed	This variable was calculated for each fragment in the study area
Matrix type	Presence of crops, African palm oil plantations and pastures surrounding the focal fragment. Only two categories were used for the analysis: pastures (includes natural savannahs and small crops) and African palm oil plantations	Aerial photographs and Google Earth images were used to assess the matrix type categories surrounding each fragment
Presence of natural fence rows	Presence of natural fence rows (defined as lines of native vegetation non-human planted used to divide pastures, Carretero-Pinzón et al. 2010)	Aerial photographs and Google Earth images were used to extract this variable by sub-regions (Figure 1)
<b>Site Scale</b>		
Average Canopy Height	Canopy height measure taken with a digital rangefinder every 200 m in each transect in the surveyed forest patches	Average of the survey sites for each of these variables was used for the fragments present

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Number of food plants consumed by each primate species	Number of all plant species found in all strips in each transect in the surveyed forest patches	in the two sub-regions showed in Figure 1.
Presence of trees with fruits	Number of trees with fruits, flowers or young leaves present at the moment of the vegetation surveys, in all strips in each transect in the surveyed forest patches	

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### Calculate costs

An important part in the process of prioritisation is the choice of cost that conservation have for particular conservation areas (Cameron et al. 2010). Surrogates to determine the cost of setting aside a particular area for conservation purposes were chosen using these alternatives: 1) equal cost (arbitrary value for all planning units), to assess if the spatial solutions of the priority process were driven by the different surrogate cost used (Luck et al. 2004); 2) the area of each planning unit (Margules et al. 1988); 3) the inverse of the distance of each planning unit to the nearest town present in the study area; and 4) A combination of area and the inverse distance of each planning unit to the nearest town. This cost was calculated by multiplying the inverse distance of the nearest town by the area of each planning unit (i.e. forest patch in the study area). All three surrogates can influence the feasibility of purchase or use that land for conservation purposes. I am assuming that areas closest to the nearest town are more expensive than areas farthest to the nearest town, independent of the size of the area. Also, I assumed that smaller areas are less costly than larger areas, based on a comparison between some farm land values available from five farms with different



sizes in a small part of my study areas (E. Enciso Com. Pers.; A. Sanchez Com. Pers 2013). I did not use the land cost as this information was not available for the study area. To be able to compare the trade-off curves for all the costs used in this analysis, I re-escalate each estimated cost as follows:

Re-escalate estimate cost =  $\text{cost} - \text{minimum cost} / \text{maximum cost} - \text{minimum cost}$

### **Identifying conservation priorities**

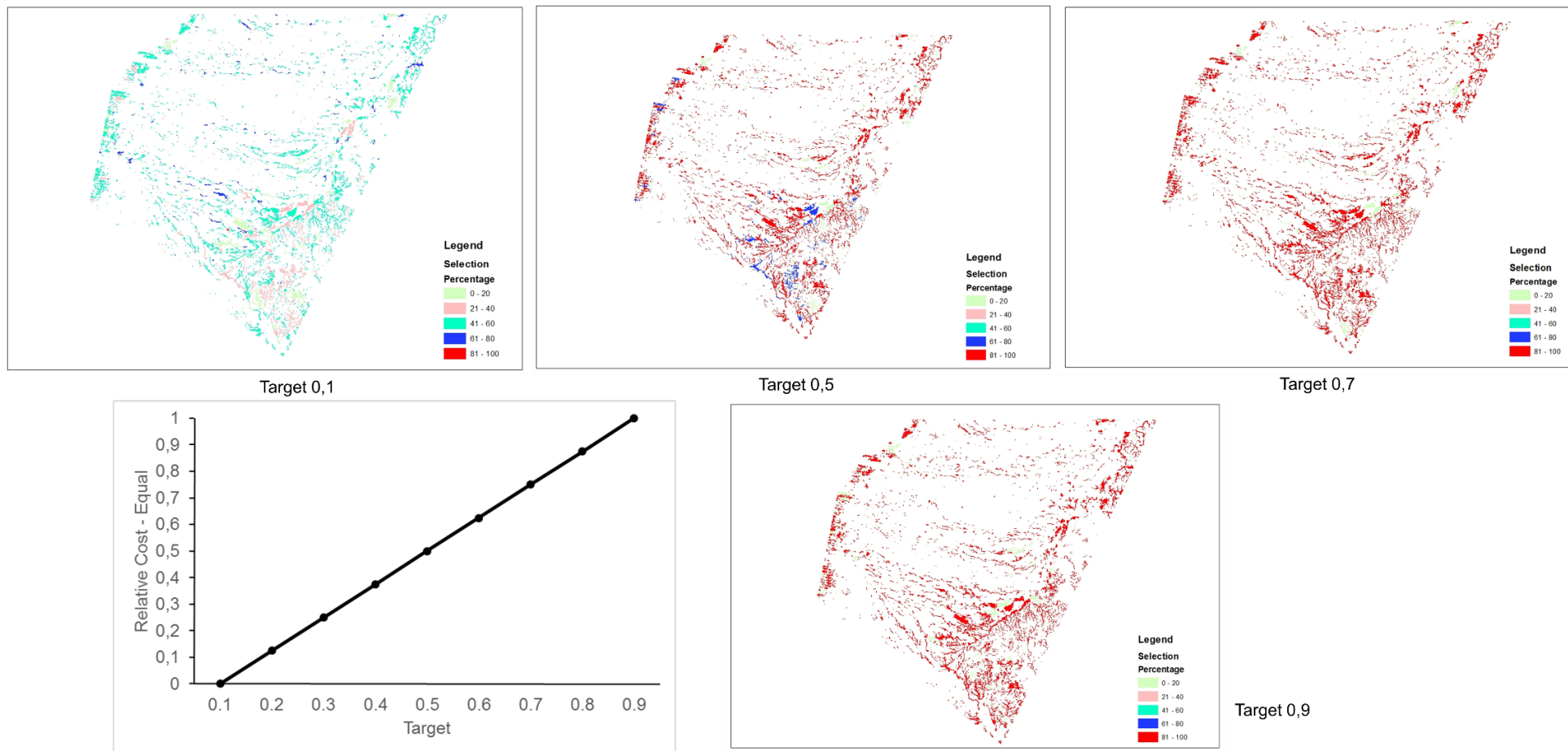
I used the systematic conservation software Marxan (version 1.8.10, Ball & Possingham 2000) to select priority conservation areas for each cost. The objective used was to minimize cost subject to the constraints that each primate species meets its conservation targets (Possingham et al. 1993, Wilson et al. 2005; Martin et al. 2010). I run Marxan 1000 times with a boundary length modifier of 0 and analyse the spatial arrangement of the selection frequencies to detect zones in the study area for primate conservation. We run Marxan between 10 % and 90 % of total abundance for each primate species, for each of the four different costs functions explained above. This allows me to evaluate the variation in the shape of relationship between different costs and conservation benefits and variation in the location of conservation priorities across the three cost functions.

## **Results**

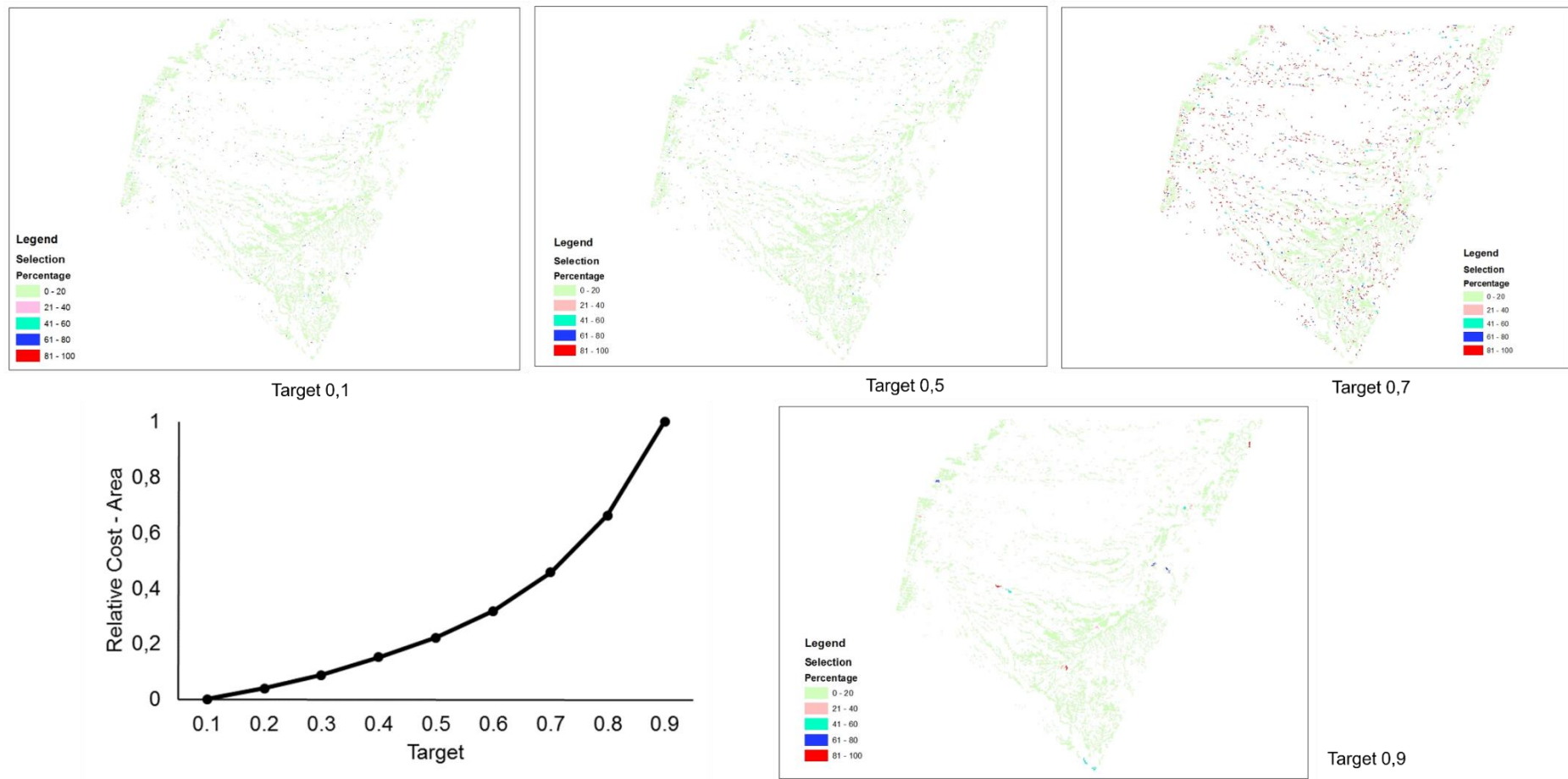
### **Selection of priority areas**

The selection of the priority areas followed a spatial pattern clearly driven by the cost used as observed by the comparison between the selection percentage of each cost (Figures 14 – 16) and the spatial arrangement of the equal cost (Figure 13). When area was used the spatial arrangement of the priority areas were more spread across the whole study area and mainly the smallest areas were selected

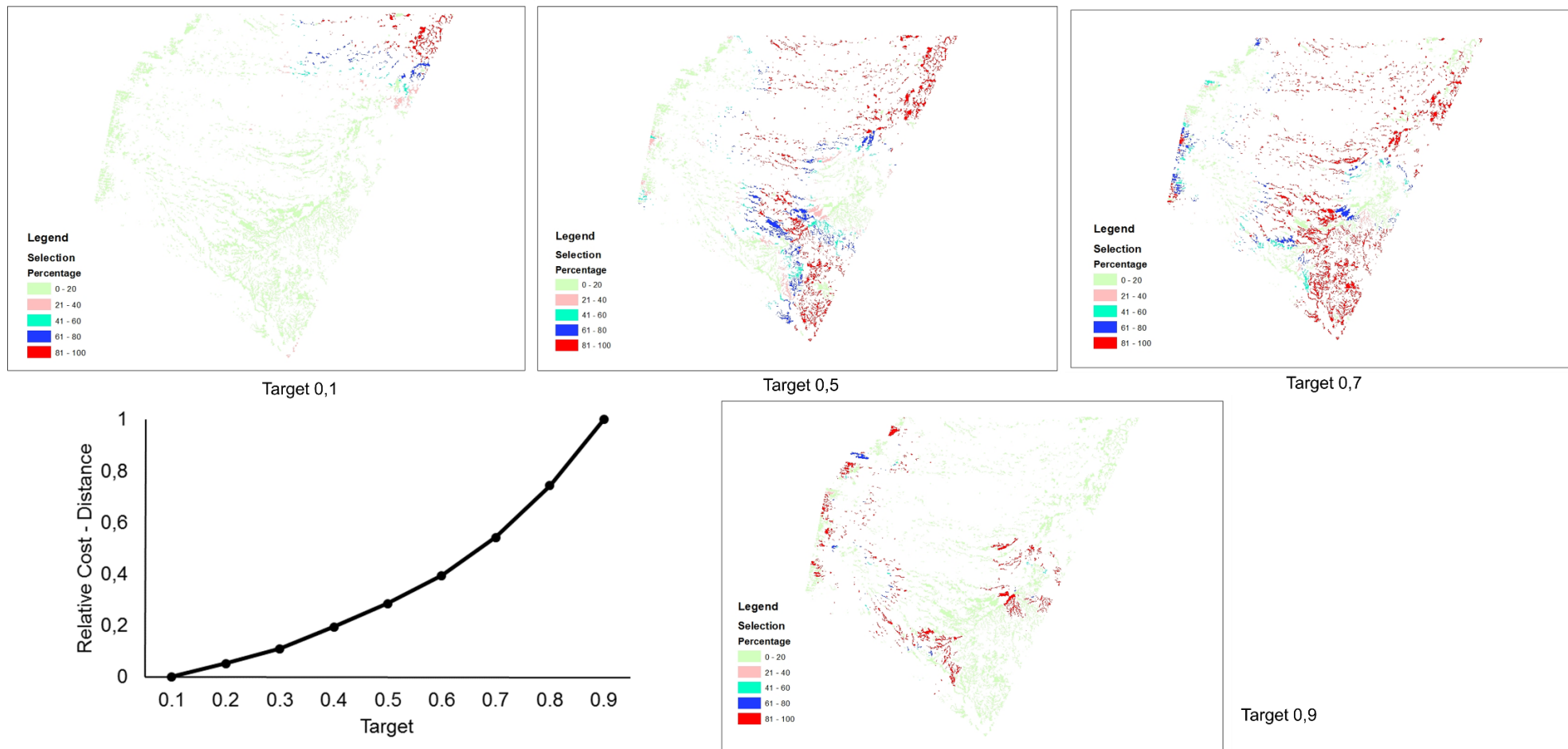
(Figure 14), for all the conservation targets, except for the highest proportion of primate abundance (target 90 % in Figure 14). On the other hand, when the inverse distance to the nearest town is used as a surrogate cost, the priority areas selected showed a spatial arrangement towards the eastern part of the study region, where there are fewer towns, for the conservation targets of 10 to 50 % (Figure 15). When the conservation target is increased to the highest value (90 %) the spatial arrangement changes to the southernmost part of the study region, where there are even fewer towns (Figure 15).



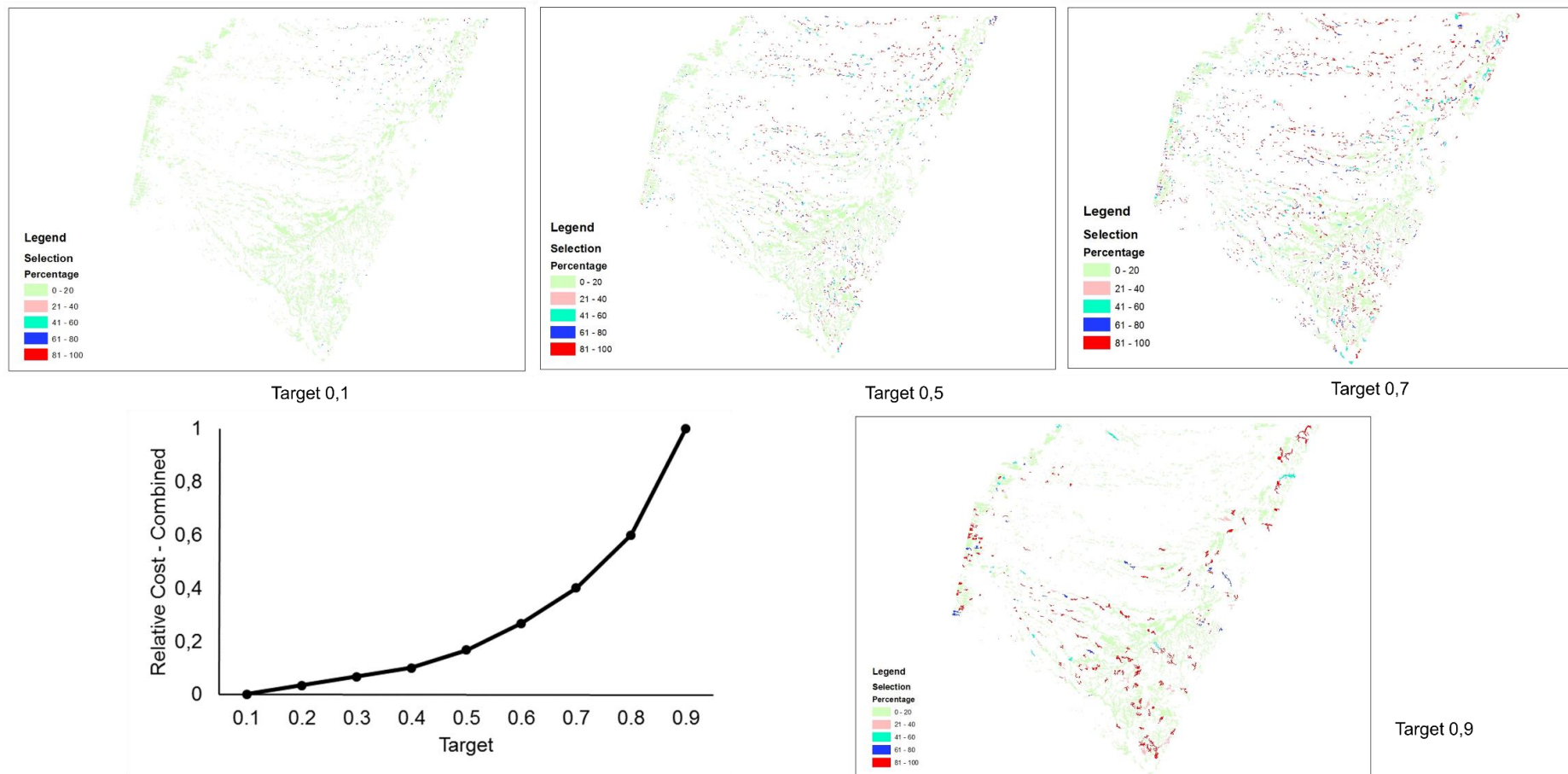
**Figure 13 Spatial representation of the selection percentage of priority conservation network for selected conservation targets when the cost is equal for all the planning units**



**Figure 14 Spatial representation of the selection percentage of priority conservation network for selected conservation targets using area as a surrogate of cost**



**Figure 15 Spatial representation of the selection percentage of priority conservation network for selected conservation targets using the inverse distance to the nearest town as a surrogate of cost.**

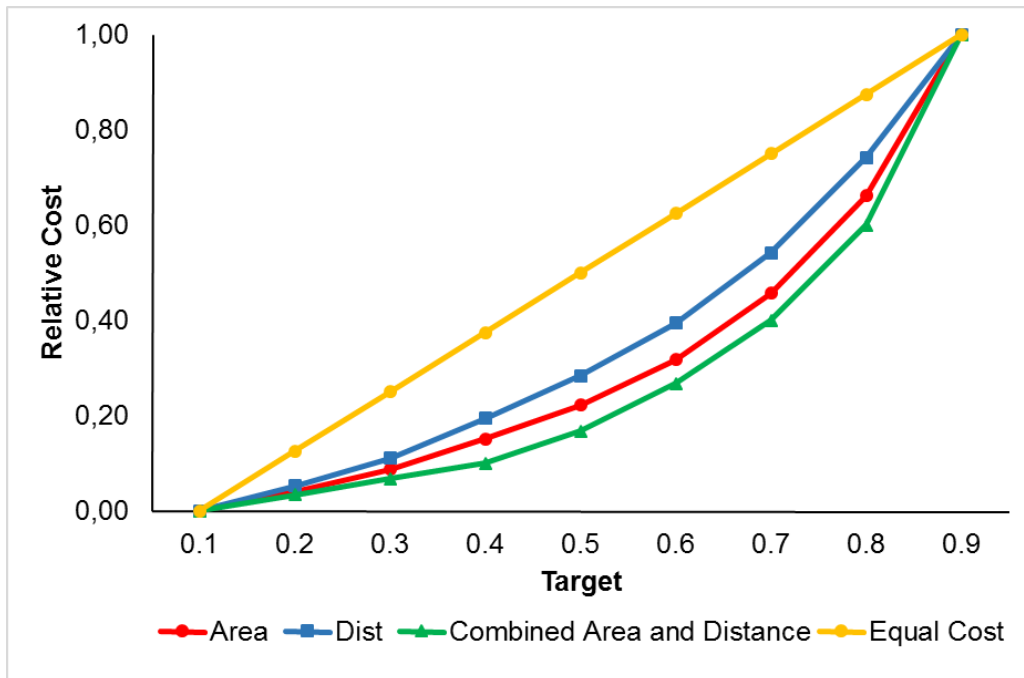


**Figure 16 Spatial representation of the selection percentage of priority conservation network for select conservation target using the combination of inverse distance to the nearest town and area as a surrogate of cost.**

The spatial arrangement of the priority areas is different again, when the combination of the inverse distance to the nearest town and area is used as a surrogate cost, to a more widespread pattern across the study region (Figure 16), for the conservation targets of 50 to 70 % (similar to Figure 15). But, when the conservation target is decreased to the lowest value (10 %) the spatial arrangement changes to the north- eastern part of the study region, where the closest town to the east is at approximately 97 km (Figure 16). Also, when the conservation target is increased to the highest value (90 %) the spatial arrangement changes to the southern part of the study region, where there are few towns (Figure 16).

### **Cost – Target Relationship**

All the selected cost analysed have the same shape, showing diminishing returns as expected (Figure 17). The trade-off curves were not much different between them except when equal cost was assumed. However, the trade-off was least strong for the area and distance combined cost and strongest when equal cost was used.



**Figure 17 Relationship between conservation target and cost for each of the four cost functions.**

## Discussion

This study aimed to assess conservation area priorities for primates in a highly fragmented part of the Colombian Llanos, and evaluate the shape of the trade-off between cost and primate abundance targets across alternative cost surrogates. This study has two main contributions. First, it highlights the importance of combining spatial models of primate abundance and distribution with conservation prioritisation tools. Second, it the importance of a careful choice of the surrogates used as costs for primate conservation under the minimum set problem (Possingham et al. 2010).

The incorporation of abundance estimates that includes species features such as group size and composition in the prioritising process allow us to consider important aspects of the sociality of primate species that may affect their long-term persistence in fragmented landscapes. Selection of priority areas for biodiversity conservation is generally based on occurrence data and distribution models that



affects the sensitivity of the conservation planning results (Wilson et al. 2005; Rondinini et al. 2006). Careful consideration of the data used to generate the distributions incorporated in the prioritization process need to be taken in account as this data present different types of errors that affects the outcomes of the conservation plans (Rondinini et al. 2006).

In the absence of actual cost data, the choice of surrogate had an important influence on priorities (Polasky et al. 2008). Such difference in the spatial arrangement of the priority areas may have important influence on the ability of conservation organizations may have to implement those conservation areas network, due to the cost involved in the implementation process (Carwardine et al. 2008; Polasky et al. 2008). Therefore, it is in this context that a good surrogate for the cost could signify the difference between the ability to propose more feasible conservation networks at reasonable cost (Naidoo et al. 2006; Cameron et al. 2010). For the study region the combination of the inverse distance to the nearest town and area as a cost was the scenario that produced most cost-effective solutions, while meeting all the targets, although not necessarily being more spatially compact in terms of their spatial arrangement.

Alternative surrogate costs could be used to determine a more compacted conservation areas network in fragmented landscapes, such as human population density (Rondinini et al. 2006; Plazas-Pinto et al. 2011) or the value of agricultural land (Armsworth 2014) that incorporates socioeconomic components relevant to highly transformed areas (Naidoo et al. 2006). However, these surrogates are not always available or may not represent the target cost variable accurately. A cost surrogate that has been considered a poor one is area, because the spatial variation in the cost of different conservation actions is ignored and does not lead to the identification of most cost-effective areas for investment (Cameron et al. 2010). However, when not cost is available the use of area as a surrogate is better than assuming an equal cost as showed by my results.

The increased deforestation and fragmentation of tropical forests has led to landscapes where forest fragments of different sizes that are immersed in a human-degraded matrix are the only habitat available for some primate species (Marsh et al. 2013). The incorporation of combined spatially explicit models and conservation planning tools for primates benefits the prioritising process by considering primate species features such as group size and composition that affects the long-term persistence of these species in fragmented areas. A clear process of prioritising conservation areas in transformed landscapes in which human activities compete with conservation, can help to negotiate and allocate resources that allow us to get most cost-effective solutions for primate conservation (Naidoo et al. 2006; Bode et al. 2008; Carwardine et al. 2008). In addition, another component in some fragmented areas, although not present in my study area in a high proportion, is the implementation of regeneration projects that can increase the habitat available and complement the spatial arrangement of that habitat for the target species (Bruton et al. 2013; Crouzeilles et al. 2015). A conservation planning analysis that incorporates the cost of implementing this strategy (areas allocated to regeneration projects) to get the conservation targets can also add value to the management actions implemented in the study area, as shown by Crouzeilles et al. (2015) for two mammal species in the Atlantic forest of Brazil. For highly fragmented landscapes, my study highlights that more cost-effective solutions can be obtained by using a combined cost of area and inverse distance to nearest towns to prioritise conservation areas for primates than the solution obtained if only area is used as a cost, when no cost information is available. In conclusion, a careful consideration of the cost surrogates needs to be taken in highly fragmented areas. For the study region considered here, the north-east and south-east parts of the study region, that concentrate a good proportion of the selected fragments, seems to be the zones in which primate conservation need to focus.

## **Chapter 6: General Discussion and Conclusion**

This thesis had four aims: 1) determine what is currently known about the effects of patch size in primates and whether or not it varies across life history traits; 2) determine the relative importance of site-scale, patch-scale and landscape-scale variables for primate species occupancy and abundance in the Colombian Llanos; 3) determine the relative importance of site-scale, patch-scale and landscape-scale variables for primate species group density, composition and size in Colombian Llanos; and 4) based on the model from (3) identify priority conservation areas for primate conservation in the Colombian Llanos, using systematic conservation planning. My findings highlight five important contributions for primate conservation. First, I made a quantification of the general effects of patch size on primate species responses finding consistent patterns on primate responses. Second, through this thesis I gained a multi-scaled understanding of the effect of landscape change on primates. Third, an expansion on the multi-scale approach lead to explicitly link landscape change simultaneously to occupancy, abundance and group structure. Fourth, I include a comparative assessment across multiple species in the same landscape. Finally, is the first study to apply a multi-scaled approach to conservation planning for primates. Below I expand on these contributions of my thesis to finish in some recommendation for future studies of primate species in fragmented landscapes.

### **Quantification of general effects of patch size on primate species responses**

Patch size is the most common predictor used in primate studies to measure the effects of habitat loss and fragmentation (Arroyo-Rodriguez et al. 2013a; Carretero-Pinzón et al. 2015). However, patch size, as a measure of both habitat loss and fragmentation make difficult to differentiate the effect of these two processes (Fahrig 2003). Life history traits have been suggested as important to predict species responses to habitat loss and fragmentation (Thornton et al. 2011; Vetter et al. 2011). In primates, life history trait has been used to predict primate species

susceptibility to habitat loss and fragmentation (Onderdok & Chapman 2000; Boyle & Smith 2010b). The main traits used to predict the susceptibility of primate species to habitat loss and fragmentation (body size, home range size, diet specialization, group size and social structure) have not been analysed together as potential intrinsic factors that influence primate species response to patch size, except for few studies with contradictory findings (Onderdonk & Chapman 2000; Boyle & Smith 2010b). The meta-analysis of the primate literature I conducted showed a consistent pattern in the primate species responses to the effect of a reduction on the patch size, without a strong evidence of being influenced by life history traits, except for parasitic prevalence and diversity, although with a weak support.

Fragmented landscapes are characterized by reduced amount of habitat, higher number of forest patches with a reduced mean size and higher distances between patches (McIntyre & Hobbs 1999; Fahrig 2003). In this fragmented landscapes, the reduction of patch size is expected to show a consistent positive correlation with density, parasitic prevalence and diversity, and time spent feeding, while species presence and genetic diversity is expected to be negative, according to the findings of my review. These consistent patterns have important consequences on primate conservation in fragmented landscapes. For example, when a decision about which landscapes to conserve for primates is needed, a better informed decision is to target landscapes in which patch sizes are larger. This strategy may reduce the negative consequences of primate population living in higher densities, with higher parasitic prevalence and diversity and where they need more time spent feeding. Similarly, based on the patterns found in my review, fragmented landscape with larger forest patches are expected to have more primate species and more genetic diversity than landscapes in which patch sizes are small. Although other factors such as hunting and logging also affect primate species persistence in fragmented landscapes (Michalski & Peres 2005), when conservation budget and time are important constraints to prioritise where to focus our conservation actions, the general patterns of primate responses observed as a consequence of patch size reduction can be a good strategy to make these decisions. I am not suggesting that

this is the best strategy and the only strategy to be used to direct primate conservation strategies, but is a starting point when not time and money is available for a more detailed monitoring of primate species.

In addition, my review showed a lack of clear defined predictors used to measure the effects of habitat loss and fragmentation. As mentioned before the main predictor used to evaluate the effects of habitat loss and fragmentation on primate species is patch size. However, habitat loss and fragmentation are landscape process that can be differentiated by using predictors measure at the landscape scale (Lustig et al. 2015). Although this finding is not new, other authors had highlighted this lack of clear predictors on primate studied before (Arroyo-Rodriguez et al. 2013b; Arroyo-Rodriguez & Fahrig 2014), I strongly recommend that future studies aimed to evaluate the effects of habitat loss and fragmentation on primate use a landscape approach and include landscape scale predictors in their sample design.

### **Value of the landscape approach to improving primate conservation**

The incorporation of clear predictors that differentiate variables affecting species responses at different scales has been demonstrated to be an important approach to study the effects that habitat loss and fragmentation have on primate species (Arroyo-Rodriguez et al. 2013b). Spatial configuration and composition of the landscape vary with the scale at which these patterns are observed and the species of study (Wiens 1989; Wiens & Milne 1989; Jackson & Fahrig 2012). In chapter 3 I showed that landscape composition as well as the scale at which that composition is measure affects differently each primate species studied.

A central concept in landscape ecology is the scale (Wu & Li 2006). The importance of analyse the scale that is appropriate for the organisms is important to understand the interaction between populations and landscape pattern (Weins & Milne 1989; Turner et al. 2001; Wu & Li 2006; Wiens 2009). In primates, only two studies had evaluated the effect of scale on spatial distribution of primate species,

finding that landscape variables affect species differently depending on the scale (Thornton et al. 2011; Arroyo-Rodriguez et al. 2013b). This was also highlighted in the analysis I made in chapter 3, as I found differences in the scale at which each primate species occupancy and abundance are affected by the landscape variables, mainly by the amount of forest around patches. Therefore, management actions for primate species in the Colombian Llanos need to be focused to increase the amount of forest cover around the patches in which primates are present with special consideration on the scale important for each primate species. Similar to what my review suggests for primates in general, my analysis also suggest that our conservation strategies for primate species need to be focused on landscapes that have more forest cover which usually have also larger patches.

The amount of forest around patches is important for primate conservation in fragmented landscapes for the four primate species studied here. This variation in the scale at which landscape variables affect each species is consistent with the dispersal distance known for the primate species studied. For example, for the two endemic species in my study area, dusky titi monkey (*C. ornatus*) and the Colombian squirrel monkey (*S. c. albigena*), conservation strategies need to be focused in landscapes with a high proportion of forest cover measured at 1000 m of spatial extent, this is the longest dispersal distance we known for these species in the study region (Carretero-Pinzón unpublished data). An increase of the amount of forest also improve the occupancy and abundance of the other two species in the study area, black-capped capuchins (*S. a. fatuellus*) and red howler monkeys (*A. seniculus*) at 1000 m spatial extent and 2500 m spatial extent, respectively. These results are consistent with an important concept in landscape ecology, context, it means that the matrix matters (Wiens 2009).

Group size and composition influence the survivorship and persistence of primate species (Terborgh & Janson 1986; Wrangham et al. 1993; Chapman & Pavelka 2005; Gogarten et al. 2015; Chapman & Valenta 2015). Therefore, in chapter 4 I explore more in detail how the spatial composition of the landscapes affects group density, size and composition for the primate species studied and compared with

the influence of site and patch scale variables. I found that the amount of forest cover at 1000 m spatial extent was important for primate species abundance (number of groups), reinforcing the importance of the landscape context. However, the interactions between individuals and populations depends not only on the landscape mosaic (i.e. context) but also on the condition inside the habitat patches (Wiens 2001; Wiens 2009). Site-scale variables related with the abundance of food resources were found to be important in determining the group size and group composition of the primate species studied. Therefore, my results from chapters 3 and 4 highlights the importance of incorporating a landscape approach in primate conservation, especially in highly fragmented landscapes.

In fragmented landscapes, a reduction in the amount of habitat will reduce the abundance of food resources available to primate groups (Cordeiro & Howe 2001; Worman & Chapman 2006). This reduction in resources can increase competition between individuals and groups and may determine the group size and composition (Terborgh & Janson 1986; Wrangham et al. 1993; Chapman & Pavelka 2005; Gogarten et al. 2015). In my analysis, although the amount of forest around patches was important for the group density of the primate species studied, it was the abundance of food resources that influence the group size and composition. This has important implications for primate conservation on fragmented landscapes. The management of primate population in this landscapes will require a clear definition of the objective of our management actions. If the group density need to be manage to reduce for example, the effects that between group competition has on primates, the management action need to focus on increasing the amount of forest around the forest patches with higher group density. However, if it is group size and composition what need to be manage to reduce within groups competition, then management actions need to focus on increase the food availability inside of forest patches. This give us clear directions to improve primate conservation that can be used in other landscapes.

## **Incorporating a landscape approach on a prioritising process for primate conservation**

The increase of deforestation in tropical areas (Hansen et al. 2013), as well as the need to establish a more connected network of conservation areas is critical for biodiversity conservation (Wiens 2008; Trombulak & Baldwin 2010). Primate conservation needs to understand the landscape process surrounding conservation areas as well as being able to include landscapes outside of those conservation areas to reverse the decline of threatened species (Marsh et al. 2013). The incorporation of concepts from landscape ecology and systematic conservation planning are a critical step in determining effective strategies for primate conservation in highly transformed landscapes (chapter 5). The prioritising process in chapter 5 incorporates the abundance predictions of the model I develop in chapter 4 to select conservation areas in highly fragmented areas of Colombian Llanos. This model is based on multiple scales (site, patch and landscape scales) that affect the group density, size and composition of the primate species studied. The inclusion of a multi-scale model in a prioritising exercise by using the predicted abundances of the species for which I want to select priority areas incorporates important components of the biology of the species in the selection process such as group size and composition of primate species. For primates, group size and composition affects many aspects of their sociality including reproductive and developmental rates, individual stress levels, disease susceptibility and individual and group behavior (Borries et al. 2008; Majolo et al. 2008; Chapman & Valenta 2015).

In addition, the findings of chapter 5 lead to an understanding of the role of cost in driving priorities for primate species in fragmented landscapes. Selection of conservation areas in highly fragmented areas are important in spite of the apparent small conservation value that landscape with different uses seems to have (Polaski et al. 2005; Polaski et al. 2008). In the absence of actual cost data, the choice of surrogate had an important influence on priorities (Polaski et al. 2008). For the study region the combination of the inverse distance to the nearest



town and area as a cost was the scenario that produced most cost-effective solutions, while meeting all the targets. For the primate species included in this study, the north-east and south-east parts of the study region, concentrate a good proportion of the fragments selected as priorities for primate conservation.

## **Management recommendations**

Most of the current national or regional primate action plans still focus only on the management of threats inside of the conservation areas (Oates et al. 2007; Ministry of Forestry 2009; Jerusalinsky et al. 2011; Dunn et al. 2014). More recently, management activities related with the landscapes in which the conservation areas are located has been also included (Valderrama & Katan 2006; Carlsen et al. 2012; IUCN & ICCN 2012; Maldonado et al. 2012). Only one of this action plans have used systematic conservation planning as part of the conservation strategy of chimpanzees in Sierra Leone (Carlsen et al. 2012). Understanding the effects that landscape change has on primate species at different scales helps us make better informed decisions for primate conservation in highly fragmented areas. The incorporation of a landscape approach, such as the one used in this thesis, in which multiple scales are analyzed increase our ability to detect threats and processes affecting primate species in a clear way. This allow us to make specific management recommendations that can be discussed and incorporated in conservation plans for primates and other species in the Neotropics. Management actions such as implementation of regeneration and reforestation projects that lead to increase the amount of forest cover in the landscapes will lead to an increase in occurrence and abundance of the primate species studied in this thesis.

Forest cover as well as food resource abundance and the matrix surrounding forest patches determines the spatial distribution and abundance of primate species living in highly fragmented landscapes. In these landscapes, conservation actions that increase the connectivity as well as the amount of forest cover are necessary to

improve the long term persistence of primate species. Consideration of the scale at which this actions are taken have to be connected to the specific scales at which those species are most affected (chapter 3). For example, changes in the amount of forest cover around patches at 1000 m buffer distance are relevant for dusky titi monkeys, black-capped capuchins and the Colombian squirrel monkey occurrence and abundance, while changes in the same variable at 2500 m buffer distance are relevant for red howler monkey occurrence and abundance. Group size and composition of primate species in fragmented landscapes are influenced not only by the amount of forest but also by the conditions inside the remaining patches (chapter 4), especially for the abundance of food resources. Therefore, to reduce the negative effects of group density, management action need to focus on increasing the amount of forest around the forest patches. However, if the reduction of the effect of group size and composition is the objective then food abundance resources need to be increased inside of the forest patches.

In fragmented landscapes, the viability of conservation areas implementation depends on the cost of that implementation, therefore it is important to include it in the priority process (Polaski et al. 2008). A systematic conservation planning process that incorporates the explicit spatial distribution of primate species can better inform conservation decision for primates in fragmented areas. This approach also allows us to identify priority areas that can be used in workshops of expert knowledge consultation, commonly used in primate conservation plans (Carlsen et al. 2012; IUCN & ICCN 2012; Maldonado et al. 2012), to assess the viability of the implementation of these priority areas. My results in chapter 5 highlights the importance to choosing conservation areas towards zones with less towns and more forest cover for primate conservation, based on the cost surrogates used in my analysis. In the study area, zones with these features are found in larger farms towards the west. This is important to be considered in the conservation plans that need to be develop for two of the primate species studied here (*Callicebus ornatus* and *Saimiri cassiquiarensis albigena*), as around 50 % of the distribution of these species is contained within the study area used in my prioritisation process (Defler 2010; Carretero-Pinzón 2013b; Carretero-Pinzón et al.

2013). A similar approach could be used for other Neotropical primates that are only found in fragmented landscapes and that need consideration of the trade-offs between conservation and economic activities. This trade-off is particularly important in my study area as it is one of the expansion areas for petroleum resource exploitation, palm oil plantations and cattle ranching.

## **Limitations and Future Directions**

This thesis used a landscape ecology approach to assess the relative role of landscape, patch and site scale variables on primate occurrence, abundance, group size and composition at different scales and how this approach can be incorporated in a prioritization process of conservation areas for primates. Because my findings highlight the importance of different actions at different scales, a prioritising process in which actions at different scales can be incorporated could be more accurate. One possibility to do this is the use of prioritising software that include a zonation of management action in the priority areas selection such as Marxan with zones (Watts et al. 2009). Here I discuss some of the limitations and research future direction that I consider have to be incorporated in primate studies in fragmented landscapes.

Future research of primate species in fragmented landscapes not only need to continue using a landscape approach as the one used in this thesis, but also include additional landscape variables that measure habitat loss and fragmentation simultaneously to disentangle their effect on primates. Future research on multiple species, inhabiting fragmented landscapes, with variable life history traits in which predictor that allow us to separate the effect of habitat loss and fragmentation are needed. Additional research to evaluate the value of regenerating areas in fragmented landscapes could be useful (Bowen et al. 2007), as the implementation of this strategy is globally used (Menz et al. 2013; Crouzeilles et al. 2015).

The finding in this thesis are limited to a subset of primate species that are adapted to naturally fragmented forest such as the gallery forest present in the Colombian Llanos. Therefore, a landscape approach to assess the effect of habitat loss and

fragmentation for primate species that are highly dependent of dense primary forest with higher productivity such as woolly monkeys (*Lagothrix* spp.) and spider monkeys (*Ateles* spp.) is urgently needed to establish fragmentation thresholds that allow us to conserve viable population of those species.

The effect of roads has showed important impact on fauna (Trombulak & Frissell 2000; Roger et al. 2011; Rhodes et al. 2014), however its effect on primates living in fragmented landscapes is poorly understood. The inclusion of this variable in spatially explicit models could help us to understand its effects on primate species living in fragmented landscape. This can be particularly important in my study region as it is an area of high importance for agro-commodities and petroleum resource exploitation (Fedepalma 2014; Ecopetrol 2015) and these activities increase road density.

Basic information of diet for some primate species is still poor (Defler 2010). Food resource abundance was an important habitat variable when modelling the effects of landscape change on primate group size and composition, therefore a good understanding and knowledge of basic ecology of the species included in the modelling is necessary. This can be challenging for some primate species in fragmented landscapes of which no information is available and can be time consuming to obtain it. A solution to this limitation is the use of similar species information in the modelling process, however caution needs to be taken to choose the sources of that information and the appropriate species of reference.

Exploration of the viability in the implementation of the priority conservation areas selected in the systematic conservation planning process applied in chapter 5, would be the first step in implementing a transparent framework to assess priority conservation areas in fragmented landscapes for primates in Colombia. Future studies incorporating alternative surrogates of cost such as agricultural land cost as planning units could be useful to prioritise areas in fragmented areas similar to the study area. The priority conservation areas identified in the prioritising process in chapter 5, need to incorporate an expert and stakeholder consultation process to assess the benefits of the priority areas selected. The incorporation of combined

spatially explicit models based on predicted abundance and conservation planning tools that incorporates a landscape approach are highly recommended for other primate species occurring in fragmented landscapes.

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## Appendix

### Appendix A. Primate Species in the study area (Chapter 1).



**Colombian Squirrel Monkey**  
(*Saimiri cassiquiarensis albigena*)



**Brumback Night Monkey**  
(*Aotus brumbacki*)



**Dusky Titi Monkey**  
(*Callicebus ornatus*)



**Black-capped Capuchin Monkey**  
(*Sapajus apella fatuellus*)



**Red Howler Monkey**  
(*Alouatta seniculus*)

**Appendix B. References included for each response variables used to evaluate the effect of habitat loss and fragmentation across traits and the predictors used for each study included (Chapter 2).**

Predictor used in those papers	Response						
	Density	Parasitic prevalence and diversity	Presence	Genetic diversity	Time spent feeding	Time spent resting	Time spent moving
Patch size			1, 4, 5, 7, 12, 14, 15, 21, 26,				
	2, 3, 21, 22, 23, 24, 25, 27,		27, 30, 32, 33, 34, 43, 48,		2, 13, 18, 19,		2, 13, 16,
	30, 31, 44, 49, 50, 51, 53, 54,		50, 51, 52, 53, 62, 67, 68,		20, 25, 28, 29,		18, 19, 20,
	56, 57, 60, 74, 76, 80, 84, 86,		69, 70, 73, 78, 88, 89, 91,		40, 42, 46, 52,		25, 29, 40,
	87, 92, 95, 97, 100, 102, 103,	11, 16, 17, 22, 24, 27,	93, 96, 98,99, 100, 101, 102,	6, 9, 10,15,	58, 59, 61, 63,		41, 44, 52,
	105, 111, 112, 113, 114, 116,	35, 37, 38, 45, 55, 75,	103, 104, 105, 106, 107,	36, 39, 79, 92,	64, 66, 77, 83,	2, 19, 20, 25,	58, 61, 65,
	122, 123, 125, 126, 131, 132,	71, 72, 82, 93, 117,	108, 115, 118, 123, 124,	94, 109, 110,	85, 90, 120,	29, 40, 61, 83,	83, 90, 120,
Patch size	134, 135	119	125, 129, 130, 132, 133	111, 128	121, 127	90, 127	121, 127
Distance to nearest fragment			4, 5, 12, 14, 15, 30, 50, 68,	9, 10, 15, 36,			
	30, 50, 92	24	78, 88, 91, 104, 108, 115,	39, 79, 92,			
			130	110, 128	13, 25	25	13, 25
Distance to nearest town		38	43, 78, 115				
Patch shape	123	38	4, 78, 88, 91, 123	110			
Forest Cover	123	119	4, 5, 69, 88, 123, 133	110			
Edge density	123		123				
Mean inter-patch isolation distance	123		123				
Number of forest patches	123		4, 88,	110			
Matrix	3, 31, 54, 123		3, 5, 7, 14, 26, 123, 129,	6, 9, 10	58, 120		58, 120

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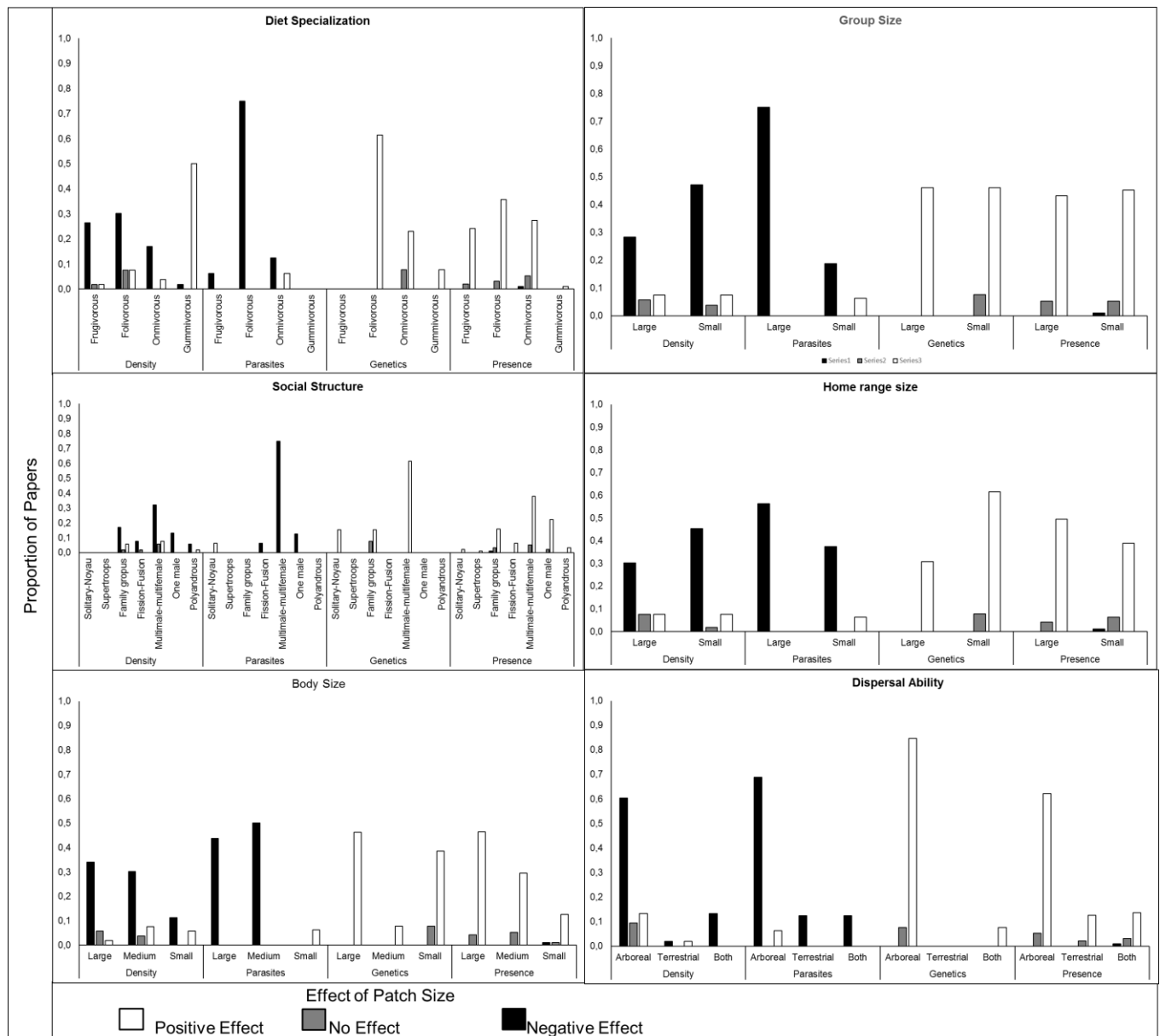
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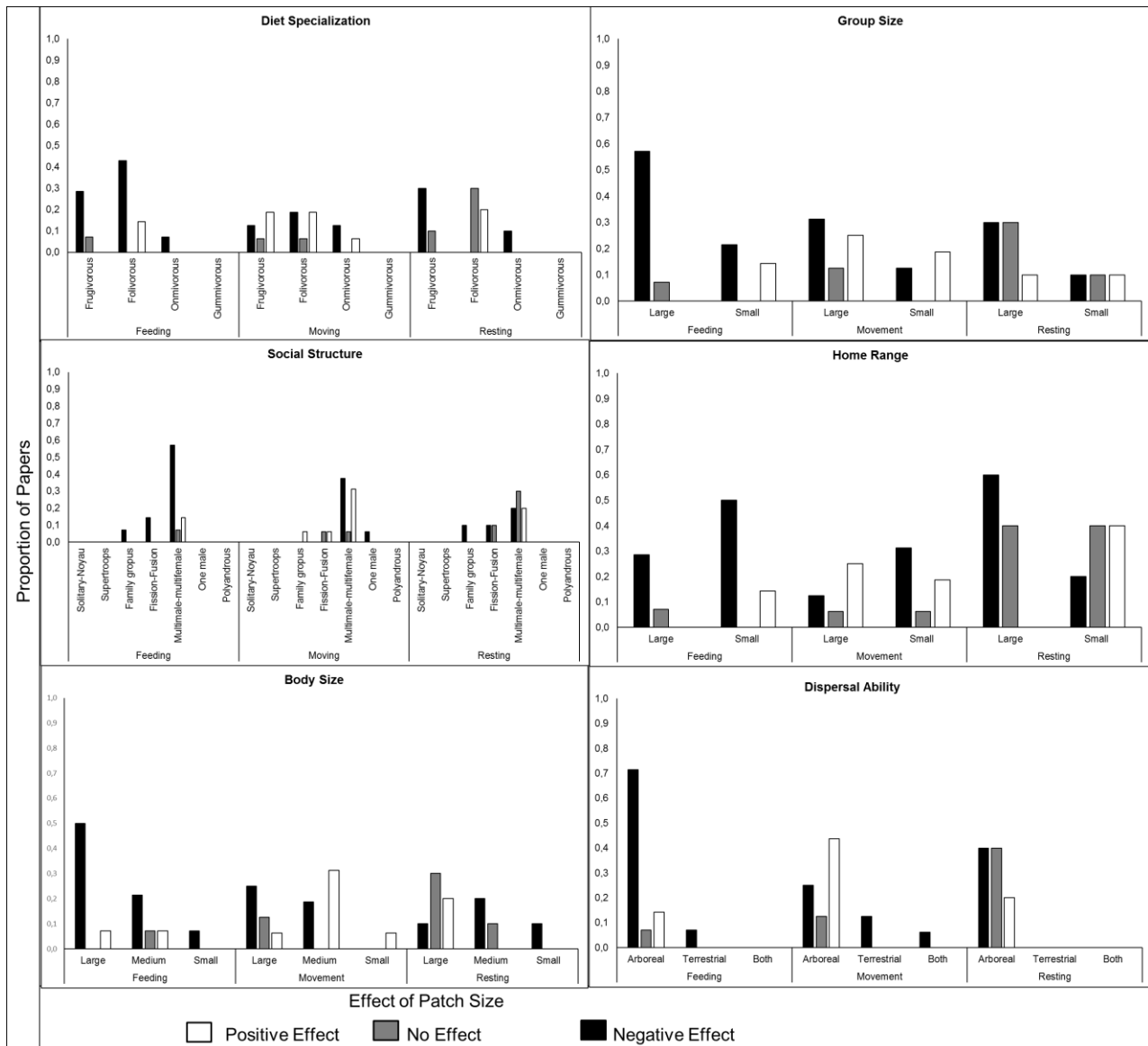
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**Appendix C. Additional graphics of all the response variables studied across traits.  
(Chapter 2).**



**Figure C.1. Effect of patch size on density, presence, parasitic prevalence and diversity, and genetic diversity across primate species traits.**



**Figure C.2. Effects of patch size on behavior (movement, resting and feeding activities) analyzed across primate species traits.**

**Appendice D. JAG Code (D.1) and R Code (D.2) of the Bayesian state-space model to evaluate the importance and effect size of site-scale, patch-scale and landscape-scale variables on group density, group size and group composition of primate species in the Colombian Llanos (Chapter 4).**

**D.1. JAG Code**

```
model {  
  
#NUMBER OF GROUPS  
for (i in 1:CSITES)  
{  
    #process model  
    G[i,1] ~ dpois(lambda[i])  
    lambda[i] <- exp(sum(X[i,] * alpha))  
    #observation model  
    for (j in 1:NSURVEYS[i,1])  
    {  
        NGROUPS[i,j] ~ dbin(p,G[i,1])  
    }  
}  
  
#GROUP SIZE AND COMPOSITION  
Con <- 0  
for (i in 1:CGROUPS)  
{  
    #group size  
    zeros[i,1] ~ dpois(mu[i])  
    mu[i] <- - GSIZE[i,1] * log(eta[i]) + log(exp(eta[i]) - 1) + logfact(GSIZE[i,1]) + Con  
    log(eta[i]) <- sum(Y[SITE[i,1],] * beta)  
  
    #composition - females, males, immatures  
    COMP[i,] ~ dmulti(q[i,],GSIZE[i,1])  
    #specify functional forms for cause probabilities  
    for (j in 1:4) #set theta[1] = 1 in priors  
    {
```

```

        q[i,j] <- theta[i,j] / sum(theta[i,1:4])
    }
    for (j in 2:3)
    {
        log(theta[i,j]) <- sum(Z[SITE[i,1],] * gamma[j - 1,]) + GSIZE[i,1] * gam_size[j -
1]
    }
    log(theta[i,4]) <- c
}

#priors
for (i in 1:Nx)
{
    alpha[i] ~ dnorm(0,0.001)
}
for (i in 1:Ny)
{
    beta[i] ~ dnorm(0,0.001)
}

for (i in 1:CGROUPS)
{
    log(theta[i,1]) <- 0
}
c ~ dnorm(0,0.001)
for (j in 1:2)
{
    for(k in 1:Nz)
    {
        gamma[j,k] ~ dnorm(0,0.001)
    }
    gam_size[j] ~ dnorm(0,0.001)
}
p ~ dunif(0,1)
}

```

## D.2 R Code

```
# libraries and functions
library(runjags)
library(rjags)
library(coda)
library(snowfall)
library(parallel)
library(modeest)

setwd("~/R/Work/Chapter3")
source("../code/functions.r")

# load data objects
NGROUPS <- read.csv("~/R/Work/Chapter3/Alouatta/NGROUPS.csv")
SITE <- read.csv("~/R/Work/Chapter3/Alouatta/SITE.csv")
COMP <- read.csv("~/R/Work/Chapter3/Alouatta/COMP.csv")
GSIZE <- read.csv("~/R/Work/Chapter3/Alouatta/GSIZE.csv")
NSURVEYS <- read.csv("~/R/Work/Chapter3/Alouatta/NSURVEYS.csv")
Covariates <- read.csv("~/R/Work/Chapter3/Alouatta/Covariates.csv")

#set up covariates
X <- matrix(NA,nrow=nrow(Covariates),ncol=22)
Y <- matrix(NA,nrow=nrow(Covariates),ncol=22)
Z <- matrix(NA,nrow=nrow(Covariates),ncol=22)

#fill X
# 1's - 1
X[,1] <- matrix(1,nrow=nrow(Covariates),ncol=1)
# index
idx_x <- 2
# fragment size - 2
X[idx_x,] <- (Covariates[,1] - mean(as.vector(Covariates[,1]))) /
sd(as.vector(Covariates[,1]))
idx_x <- idx_x + 1
# plants - 3
```

```

X[,idx_x]      <-      (Covariates[,2]      -      mean(as.vector(Covariates[,2])))      /
sd(as.vector(Covariates[,2]))
idx_x <- idx_x + 1
# canopy height - 4
X[,idx_x]      <-      (Covariates[,3]      -      mean(as.vector(Covariates[,3])))      /
sd(as.vector(Covariates[,3]))
idx_x <- idx_x + 1
# canopy cover - 5
X[,idx_x]      <-      (Covariates[,4]      -      mean(as.vector(Covariates[,4])))      /
sd(as.vector(Covariates[,4]))
idx_x <- idx_x + 1
# % cover 500m - 6
X[,idx_x]      <-      (Covariates[,5]      -      mean(as.vector(Covariates[,5])))      /
sd(as.vector(Covariates[,5]))
idx_x <- idx_x + 1
# patch density 500m - 7
X[,idx_x]      <-      (Covariates[,6]      -      mean(as.vector(Covariates[,6])))      /
sd(as.vector(Covariates[,6]))
idx_x <- idx_x + 1
# patch density 1000m - 8
X[,idx_x]      <-      (Covariates[,7]      -      mean(as.vector(Covariates[,7])))      /
sd(as.vector(Covariates[,7]))
idx_x <- idx_x + 1
# % cover 1000m - 9
X[,idx_x]      <-      (Covariates[,8]      -      mean(as.vector(Covariates[,8])))      /
sd(as.vector(Covariates[,8]))
idx_x <- idx_x + 1
# patch density 2500m - 10
X[,idx_x]      <-      (Covariates[,9]      -      mean(as.vector(Covariates[,9])))      /
sd(as.vector(Covariates[,9]))
idx_x <- idx_x + 1
# % cover 2500m - 11
X[,idx_x]      <-      (Covariates[,10]     -      mean(as.vector(Covariates[,10])))      /
sd(as.vector(Covariates[,10]))
idx_x <- idx_x + 1

```

```

# matrix - 12
X[,idx_x] <- ifelse(Covariates[,11]==1,0,1)
idx_x <- idx_x + 1
# hedgerows - 13
X[,idx_x] <- ifelse(Covariates[,12]==1,0,1)
idx_x <- idx_x + 1
# basal area - 14
X[,idx_x] <- (Covariates[,13] - mean(as.vector(Covariates[,13]))) /
sd(as.vector(Covariates[,13]))
idx_x <- idx_x + 1
# fruit - 15
X[,idx_x] <- (Covariates[,14] - mean(as.vector(Covariates[,14]))) /
sd(as.vector(Covariates[,14]))
idx_x <- idx_x + 1
# flowers - 16
X[,idx_x] <- (Covariates[,15] - mean(as.vector(Covariates[,15]))) /
sd(as.vector(Covariates[,15]))
idx_x <- idx_x + 1
# young leaves - 17
X[,idx_x] <- (Covariates[,16] - mean(as.vector(Covariates[,16]))) /
sd(as.vector(Covariates[,16]))
idx_x <- idx_x + 1
# tree density - 18
X[,idx_x] <- (Covariates[,17] - mean(as.vector(Covariates[,17]))) /
sd(as.vector(Covariates[,17]))
idx_x <- idx_x + 1
# No food trees - 19
X[,idx_x] <- (Covariates[,18] - mean(as.vector(Covariates[,18]))) /
sd(as.vector(Covariates[,18]))
idx_x <- idx_x + 1
# BA FT - 20
X[,idx_x] <- (Covariates[,19] - mean(as.vector(Covariates[,19]))) /
sd(as.vector(Covariates[,19]))
idx_x <- idx_x + 1
# No stumps - 21

```

```

X[,idx_x]      <-      (Covariates[,20]      -      mean(as.vector(Covariates[,20])))      /
sd(as.vector(Covariates[,20]))
idx_x <- idx_x + 1
# shape index - 22
X[,idx_x]      <-      (Covariates[,21]      -      mean(as.vector(Covariates[,21])))      /
sd(as.vector(Covariates[,21]))
idx_x <- idx_x + 1
#fill Y
# 1's - 1
Y[,1] <- matrix(1,nrow=nrow(Covariates),ncol=1)
# index
idx_y <- 2
# fragment size - 2
Y[,idx_y]      <-      (Covariates[,1]      -      mean(as.vector(Covariates[,1])))      /
sd(as.vector(Covariates[,1]))
idx_y <- idx_y + 1
# plants - 3
Y[,idx_y]      <-      (Covariates[,2]      -      mean(as.vector(Covariates[,2])))      /
sd(as.vector(Covariates[,2]))
idx_y <- idx_y + 1
# canopy height - 4
Y[,idx_y]      <-      (Covariates[,3]      -      mean(as.vector(Covariates[,3])))      /
sd(as.vector(Covariates[,3]))
idx_y <- idx_y + 1
# canopy cover - 5
Y[,idx_y]      <-      (Covariates[,4]      -      mean(as.vector(Covariates[,4])))      /
sd(as.vector(Covariates[,4]))
idx_y <- idx_y + 1
# % cover 500m - 6
Y[,idx_y]      <-      (Covariates[,5]      -      mean(as.vector(Covariates[,5])))      /
sd(as.vector(Covariates[,5]))
idx_y <- idx_y + 1
# patch density 500m - 7
Y[,idx_y]      <-      (Covariates[,6]      -      mean(as.vector(Covariates[,6])))      /
sd(as.vector(Covariates[,6]))

```



```

idx_y <- idx_y + 1
# patch density 1000m - 8
Y[,idx_y] <- (Covariates[,7] - mean(as.vector(Covariates[,7]))) /
sd(as.vector(Covariates[,7]))
idx_y <- idx_y + 1
# % cover 1000m - 9
Y[,idx_y] <- (Covariates[,8] - mean(as.vector(Covariates[,8]))) /
sd(as.vector(Covariates[,8]))
idx_y <- idx_y + 1
# patch density 2500m - 10
Y[,idx_y] <- (Covariates[,9] - mean(as.vector(Covariates[,9]))) /
sd(as.vector(Covariates[,9]))
idx_y <- idx_y + 1
# % cover 2500m - 11
Y[,idx_y] <- (Covariates[,10] - mean(as.vector(Covariates[,10]))) /
sd(as.vector(Covariates[,10]))
idx_y <- idx_y + 1
# matrix - 12
Y[,idx_y] <- ifelse(Covariates[,11]==1,0,1)
idx_y <- idx_y + 1
# hedgerows - 13
Y[,idx_y] <- ifelse(Covariates[,12]==1,0,1)
idx_y <- idx_y + 1
# basal area - 14
Y[,idx_y] <- (Covariates[,13] - mean(as.vector(Covariates[,13]))) /
sd(as.vector(Covariates[,13]))
idx_y <- idx_y + 1
# fruit - 15
Y[,idx_y] <- (Covariates[,14] - mean(as.vector(Covariates[,14]))) /
sd(as.vector(Covariates[,14]))
idx_y <- idx_y + 1
# flowers - 16
Y[,idx_y] <- (Covariates[,15] - mean(as.vector(Covariates[,15]))) /
sd(as.vector(Covariates[,15]))
idx_y <- idx_y + 1

```

```

# young leaves - 17
Y[,idx_y] <- (Covariates[,16] - mean(as.vector(Covariates[,16]))) /
sd(as.vector(Covariates[,16]))
idx_y <- idx_y + 1
# tree density - 18
Y[,idx_y] <- (Covariates[,17] - mean(as.vector(Covariates[,17]))) /
sd(as.vector(Covariates[,17]))
idx_y <- idx_y + 1
# No food trees - 19
Y[,idx_y] <- (Covariates[,18] - mean(as.vector(Covariates[,18]))) /
sd(as.vector(Covariates[,18]))
idx_y <- idx_y + 1
# BA FT - 20
Y[,idx_y] <- (Covariates[,19] - mean(as.vector(Covariates[,19]))) /
sd(as.vector(Covariates[,19]))
idx_y <- idx_y + 1
# No stumps - 21
Y[,idx_y] <- (Covariates[,20] - mean(as.vector(Covariates[,20]))) /
sd(as.vector(Covariates[,20]))
idx_y <- idx_y + 1
# shape index - 22
Y[,idx_y] <- (Covariates[,21] - mean(as.vector(Covariates[,21]))) /
sd(as.vector(Covariates[,21]))
idx_y <- idx_y + 1
#fill Z
# 1's - 1
Z[,1] <- matrix(1,nrow=nrow(Covariates),ncol=1)
# index
idx_z <- 2
# fragment size - 2
Z[,idx_z] <- (Covariates[,1] - mean(as.vector(Covariates[,1]))) /
sd(as.vector(Covariates[,1]))
idx_z <- idx_z + 1
# plants - 3

```

```

Z[,idx_z]      <-      (Covariates[,2]      -      mean(as.vector(Covariates[,2])))      /
sd(as.vector(Covariates[,2]))
idx_z <- idx_z + 1
# canopy height - 4
Z[,idx_z]      <-      (Covariates[,3]      -      mean(as.vector(Covariates[,3])))      /
sd(as.vector(Covariates[,3]))
idx_z <- idx_z + 1
# canopy cover - 5
Z[,idx_z]      <-      (Covariates[,4]      -      mean(as.vector(Covariates[,4])))      /
sd(as.vector(Covariates[,4]))
idx_z <- idx_z + 1
# % cover 500m - 6
Z[,idx_z]      <-      (Covariates[,5]      -      mean(as.vector(Covariates[,5])))      /
sd(as.vector(Covariates[,5]))
idx_z <- idx_z + 1
# patch density 500m - 7
Z[,idx_z]      <-      (Covariates[,6]      -      mean(as.vector(Covariates[,6])))      /
sd(as.vector(Covariates[,6]))
idx_z <- idx_z + 1
# patch density 1000m - 8
Z[,idx_z]      <-      (Covariates[,7]      -      mean(as.vector(Covariates[,7])))      /
sd(as.vector(Covariates[,7]))
idx_z <- idx_z + 1
# % cover 1000m - 9
Z[,idx_z]      <-      (Covariates[,8]      -      mean(as.vector(Covariates[,8])))      /
sd(as.vector(Covariates[,8]))
idx_z <- idx_z + 1
# patch density 2500m - 10
Z[,idx_z]      <-      (Covariates[,9]      -      mean(as.vector(Covariates[,9])))      /
sd(as.vector(Covariates[,9]))
idx_z <- idx_z + 1
# % cover 2500m - 11
Z[,idx_z]      <-      (Covariates[,10]     -      mean(as.vector(Covariates[,10])))      /
sd(as.vector(Covariates[,10]))
idx_z <- idx_z + 1

```

```

# matrix - 12
Z[,idx_z] <- ifelse(Covariates[,11]==1,0,1)
idx_z <- idx_z + 1
# hedgerows - 13
Z[,idx_z] <- ifelse(Covariates[,12]==1,0,1)
idx_z <- idx_z + 1
# basal area - 14
Z[,idx_z] <- (Covariates[,13] - mean(as.vector(Covariates[,13]))) /
sd(as.vector(Covariates[,13]))
idx_z <- idx_z + 1
# fruit - 15
Z[,idx_z] <- (Covariates[,14] - mean(as.vector(Covariates[,14]))) /
sd(as.vector(Covariates[,14]))
idx_z <- idx_z + 1
# flowers - 16
Z[,idx_z] <- (Covariates[,15] - mean(as.vector(Covariates[,15]))) /
sd(as.vector(Covariates[,15]))
idx_z <- idx_z + 1
# young leaves - 17
Z[,idx_z] <- (Covariates[,16] - mean(as.vector(Covariates[,16]))) /
sd(as.vector(Covariates[,16]))
idx_z <- idx_z + 1
# tree density - 18
Z[,idx_z] <- (Covariates[,17] - mean(as.vector(Covariates[,17]))) /
sd(as.vector(Covariates[,17]))
idx_z <- idx_z + 1
# No food trees - 19
Z[,idx_z] <- (Covariates[,18] - mean(as.vector(Covariates[,18]))) /
sd(as.vector(Covariates[,18]))
idx_z <- idx_z + 1
# BA FT - 20
Z[,idx_z] <- (Covariates[,19] - mean(as.vector(Covariates[,19]))) /
sd(as.vector(Covariates[,19]))
idx_z <- idx_z + 1
# No stumps - 21

```

```

Z[,idx_z]      <-      (Covariates[,20]      -      mean(as.vector(Covariates[,20])))      /
sd(as.vector(Covariates[,20]))
idx_z <- idx_z + 1
# shape index - 22
Z[,idx_z]      <-      (Covariates[,21]      -      mean(as.vector(Covariates[,21])))      /
sd(as.vector(Covariates[,21]))
idx_z <- idx_z + 1

X_temp <- X[,c(1,2,4,9,12,13,15,19)]
Y_temp <- Y[,c(1,2,4,9,12,13,15,19)]
Z_temp <- Z[,c(1,2,4,9,12,13,15,19)]
data1                                     <-
list(NGROUPS=as.matrix(NGROUPS),COMP=as.matrix(COMP),GSIZE=as.matrix(GSIZE)
,SITE=as.matrix(SITE),NSURVEYS=as.matrix(NSURVEYS),X=X_temp,Y=Y_temp,Z=Z_te
mp,CSITES=dim(X_temp)[1],CGROUPS=dim(GSIZE)[1],Nx=dim(X_temp)[2],Ny=dim(Y_te
mp)[2],Nz=dim(Z_temp)[2],zeros=matrix(0,nrow=dim(GSIZE)[1],ncol=1))

#combine data
data <- data1
source("../code/functions.r")
#run jags
#sfInit( parallel=TRUE,cpus=2)
#export data, functions and libraries to workers
#sfExportAll()
#sfClusterEval(library(runjags))
#sfClusterEval(library(coda))
#sfClusterEval(library(rjags))
#sfClusterEval(library(parallel))
#sfClusterEval(library(rjags))
#sfClusterEval(library(modeest))
#Jags.Fits <- sfLapply(data,get.jags)
Jags.Fit <- get.jags(data)
#sfStop()
save(Jags.Fit,file="Jags_Fit.RData")

```

**Appendice E. JAG Code (E.1) and R Code (E.2) of the Bayesian state-space model used to predict the abundance of primate species in the Colombian Llanos (Chapter 5).**

**E.1 JAG Code**

```
model {
#NUMBER OF GROUPS
for (i in 1:CSITES)
{
    #process model
    G[i,1] ~ dpois(lambda[i])
    lambda[i] <- exp(sum(X[i,] * alpha))
    #observation model
    for (j in 1:NSURVEYS[i,1])
    {
        NGROUPS[i,j] ~ dbin(p,G[i,1])
    }
}
#GROUP SIZE AND COMPOSITION
for (i in 1:CGROUPS)
{
    #group size
    zeros[i,1] ~ dpois(mu[i])
    mu[i] <- - GSIZE[i,1] * log(eta[i]) + log(exp(eta[i]) - 1) + logfact(GSIZE[i,1])
    log(eta[i]) <- sum(Y[SITE[i,1],] * beta)

    #composition - females, males, immatures
    COMP[i,] ~ dmulti(q[i,],GSIZE[i,1])
    #specify functional forms for cause probabilities
    for (j in 1:4) #set theta[1] = 1 in priors
    {
        q[i,j] <- theta[i,j] / sum(theta[i,1:4])
    }
    for (j in 2:3)
    {
```

```

        log(theta[i,j]) <- sum(Z[SITE[i,1],] * gamma[j - 1,]) + GSIZE[i,1] *
gamma_size[j - 1]
    }
    log(theta[i,4]) <- c
}

```

#### #PREDICTIONS

```

for (i in 1:CSITESP)
{
    #get expected number of groups
    lambdap[i] <- exp(sum(XP[i,] * alpha))
    #get expected group size
    log(etap[i]) <- sum(YP[i,] * beta)
    abundp[i] <- lambdap[i] * etap[i]
}

```

#### #priors

##### #alpha model selection - number of groups

```

ingps[1] <- 1
alphaT[1] ~ dnorm(0,0.001)
alpha[1] <- ingps[1] * alphaT[1]
for (i in 2:Nx)
{
    ingps[i] ~ dbern(pngps)
    alphaT[i] ~ dnorm(0,taua)
    alpha[i] <- ingps[i] * alphaT[i]
}
pngps ~ dbeta(2,8)
taua ~ dgamma(1,0.001)

```

##### #beta model selection - size of groups

```

isgps[1] <- 1
betaT[1] ~ dnorm(0,0.001)
beta[1] <- isgps[1] * alphaT[1]
for (i in 2:Ny)

```

```

{
  isgps[i] ~ dbern(psgps)
  betaT[i] ~ dnorm(0,taub)
  beta[i] <- isgps[i] * betaT[i]
}
psgps ~ dbeta(2,8)
taub ~ dgamma(1,0.001)

#gamma model selection
for (i in 1:CGROUPS)
{
  log(theta[i,1]) <- 0
}
c ~ dnorm(0,0.001)
for (j in 1:2)
{
  #gamma model selection - composition
  icip[j,1] <- 1
  gammaT[j,1] ~ dnorm(0,0.001)
  gamma[j,1] <- icip[j,1] * gammaT[j,1]

  for(k in 2:Nz)
  {
    icip[j,k] ~ dbern(pcomp[j])
    gammaT[j,k] ~ dnorm(0,taug)
    gamma[j,k] <- icip[j,k] * gammaT[j,k]
  }
  icip[j,Nz + 1] ~ dbern(pcomp[j])
  gamma_sizeT[j] ~ dnorm(0,taug)
  gamma_size[j] <- icip[j,Nz + 1] * gamma_sizeT[j]
  pcomp[j] ~ dbeta(2,8)
}
p ~ dunif(0,1)
taug ~ dgamma(1,0.001)
}

```



## E.2 R Code

```
# libraries and functions
library(runjags)
library(rjags)
library(coda)
library(snowfall)
library(parallel)
library(modeest)

setwd("E:/Projects/colombian_primates/models")
source("./prediction_code/functions.r")

# load data objects
NGROUPS <- read.csv("E:/Projects/colombian_primates/models/data_Alouatta/for_jags/NGROUPS.csv")
SITE <- read.csv("E:/Projects/colombian_primates/models/data_Alouatta/for_jags/SITE.csv")
COMP <- read.csv("E:/Projects/colombian_primates/models/data_Alouatta/for_jags/COMP.csv")
GSIZE <- read.csv("E:/Projects/colombian_primates/models/data_Alouatta/for_jags/GSIZE.csv")
NSURVEYS <- read.csv("E:/Projects/colombian_primates/models/data_Alouatta/for_jags/NSURVEYS.csv")
Covariates <- read.csv("E:/Projects/colombian_primates/models/data_Alouatta/for_jags/Covariates.csv")
Cov_Pred <- read.csv("E:/Projects/colombian_primates/models/data_Alouatta/for_jags/Covariates_Pred.csv") # for the predictions

#set up covariates
X <- matrix(NA,nrow=nrow(Covariates),ncol=22)
Y <- matrix(NA,nrow=nrow(Covariates),ncol=22)
Z <- matrix(NA,nrow=nrow(Covariates),ncol=22)
XP <- matrix(NA,nrow=nrow(Cov_Pred),ncol=22) # for the predictions
```

```
YP <- matrix(NA,nrow=nrow(Cov_Pred),ncol=22) # for the predictions
```

```
#fill X
```

```
# 1's - 1
```

```
X[,1] <- matrix(1,nrow=nrow(Covariates),ncol=1)
```

```
# index
```

```
idx_x <- 2
```

```
# fragment size - 2
```

```
X[,idx_x] <- (Covariates[,1] - mean(as.vector(Covariates[,1]))) /  
sd(as.vector(Covariates[,1]))
```

```
idx_x <- idx_x + 1
```

```
# plants - 3
```

```
X[,idx_x] <- (Covariates[,2] - mean(as.vector(Covariates[,2]))) /  
sd(as.vector(Covariates[,2]))
```

```
idx_x <- idx_x + 1
```

```
# canopy height - 4
```

```
X[,idx_x] <- (Covariates[,3] - mean(as.vector(Covariates[,3]))) /  
sd(as.vector(Covariates[,3]))
```

```
idx_x <- idx_x + 1
```

```
# canopy cover - 5
```

```
X[,idx_x] <- (Covariates[,4] - mean(as.vector(Covariates[,4]))) /  
sd(as.vector(Covariates[,4]))
```

```
idx_x <- idx_x + 1
```

```
# % cover 500m - 6
```

```
X[,idx_x] <- (Covariates[,5] - mean(as.vector(Covariates[,5]))) /  
sd(as.vector(Covariates[,5]))
```

```
idx_x <- idx_x + 1
```

```
# patch density 500m - 7
```

```
X[,idx_x] <- (Covariates[,6] - mean(as.vector(Covariates[,6]))) /  
sd(as.vector(Covariates[,6]))
```

```
idx_x <- idx_x + 1
```

```
# patch density 1000m - 8
```

```
X[,idx_x] <- (Covariates[,7] - mean(as.vector(Covariates[,7]))) /  
sd(as.vector(Covariates[,7]))
```

```
idx_x <- idx_x + 1
```

```

# % cover 1000m - 9
X[,idx_x] <- (Covariates[,8] - mean(as.vector(Covariates[,8]))) /
sd(as.vector(Covariates[,8]))
idx_x <- idx_x + 1
# patch density 2500m - 10
X[,idx_x] <- (Covariates[,9] - mean(as.vector(Covariates[,9]))) /
sd(as.vector(Covariates[,9]))
idx_x <- idx_x + 1
# % cover 2500m - 11
X[,idx_x] <- (Covariates[,10] - mean(as.vector(Covariates[,10]))) /
sd(as.vector(Covariates[,10]))
idx_x <- idx_x + 1
# matrix - 12
X[,idx_x] <- ifelse(Covariates[,11]==1,0,1)
idx_x <- idx_x + 1
# hedgerows - 13
X[,idx_x] <- ifelse(Covariates[,12]==1,0,1)
idx_x <- idx_x + 1
# basal area - 14
X[,idx_x] <- (Covariates[,13] - mean(as.vector(Covariates[,13]))) /
sd(as.vector(Covariates[,13]))
idx_x <- idx_x + 1
# fruit - 15
X[,idx_x] <- (Covariates[,14] - mean(as.vector(Covariates[,14]))) /
sd(as.vector(Covariates[,14]))
idx_x <- idx_x + 1
# flowers - 16
X[,idx_x] <- (Covariates[,15] - mean(as.vector(Covariates[,15]))) /
sd(as.vector(Covariates[,15]))
idx_x <- idx_x + 1
# young leaves - 17
X[,idx_x] <- (Covariates[,16] - mean(as.vector(Covariates[,16]))) /
sd(as.vector(Covariates[,16]))
idx_x <- idx_x + 1
# tree density - 18

```

```

X[,idx_x]      <-      (Covariates[,17]      -      mean(as.vector(Covariates[,17])))      /
sd(as.vector(Covariates[,17]))
idx_x <- idx_x + 1
# No food trees - 19
X[,idx_x]      <-      (Covariates[,18]      -      mean(as.vector(Covariates[,18])))      /
sd(as.vector(Covariates[,18]))
idx_x <- idx_x + 1
# BA FT - 20
X[,idx_x]      <-      (Covariates[,19]      -      mean(as.vector(Covariates[,19])))      /
sd(as.vector(Covariates[,19]))
idx_x <- idx_x + 1
# No stumps - 21
X[,idx_x]      <-      (Covariates[,20]      -      mean(as.vector(Covariates[,20])))      /
sd(as.vector(Covariates[,20]))
idx_x <- idx_x + 1
# shape index - 22
X[,idx_x]      <-      (Covariates[,21]      -      mean(as.vector(Covariates[,21])))      /
sd(as.vector(Covariates[,21]))
idx_x <- idx_x + 1

#fill Y
# 1's - 1
Y[,1] <- matrix(1,nrow=nrow(Covariates),ncol=1)
# index
idx_y <- 2
# fragment size - 2
Y[,idx_y]      <-      (Covariates[,1]      -      mean(as.vector(Covariates[,1])))      /
sd(as.vector(Covariates[,1]))
idx_y <- idx_y + 1
# plants - 3
Y[,idx_y]      <-      (Covariates[,2]      -      mean(as.vector(Covariates[,2])))      /
sd(as.vector(Covariates[,2]))
idx_y <- idx_y + 1
# canopy height - 4

```

```

Y[,idx_y]      <-      (Covariates[,3]      -      mean(as.vector(Covariates[,3])))      /
sd(as.vector(Covariates[,3]))
idx_y <- idx_y + 1
# canopy cover - 5
Y[,idx_y]      <-      (Covariates[,4]      -      mean(as.vector(Covariates[,4])))      /
sd(as.vector(Covariates[,4]))
idx_y <- idx_y + 1
# % cover 500m - 6
Y[,idx_y]      <-      (Covariates[,5]      -      mean(as.vector(Covariates[,5])))      /
sd(as.vector(Covariates[,5]))
idx_y <- idx_y + 1
# patch density 500m - 7
Y[,idx_y]      <-      (Covariates[,6]      -      mean(as.vector(Covariates[,6])))      /
sd(as.vector(Covariates[,6]))
idx_y <- idx_y + 1
# patch density 1000m - 8
Y[,idx_y]      <-      (Covariates[,7]      -      mean(as.vector(Covariates[,7])))      /
sd(as.vector(Covariates[,7]))
idx_y <- idx_y + 1
# % cover 1000m - 9
Y[,idx_y]      <-      (Covariates[,8]      -      mean(as.vector(Covariates[,8])))      /
sd(as.vector(Covariates[,8]))
idx_y <- idx_y + 1
# patch density 2500m - 10
Y[,idx_y]      <-      (Covariates[,9]      -      mean(as.vector(Covariates[,9])))      /
sd(as.vector(Covariates[,9]))
idx_y <- idx_y + 1
# % cover 2500m - 11
Y[,idx_y]      <-      (Covariates[,10]     -      mean(as.vector(Covariates[,10])))      /
sd(as.vector(Covariates[,10]))
idx_y <- idx_y + 1
# matrix - 12
Y[,idx_y] <- ifelse(Covariates[,11]==1,0,1)
idx_y <- idx_y + 1
# hedgerows - 13

```

```

Y[,idx_y] <- ifelse(Covariates[,12]==1,0,1)
idx_y <- idx_y + 1
# basal area - 14
Y[,idx_y] <- (Covariates[,13] - mean(as.vector(Covariates[,13]))) /
sd(as.vector(Covariates[,13]))
idx_y <- idx_y + 1
# fruit - 15
Y[,idx_y] <- (Covariates[,14] - mean(as.vector(Covariates[,14]))) /
sd(as.vector(Covariates[,14]))
idx_y <- idx_y + 1
# flowers - 16
Y[,idx_y] <- (Covariates[,15] - mean(as.vector(Covariates[,15]))) /
sd(as.vector(Covariates[,15]))
idx_y <- idx_y + 1
# young leaves - 17
Y[,idx_y] <- (Covariates[,16] - mean(as.vector(Covariates[,16]))) /
sd(as.vector(Covariates[,16]))
idx_y <- idx_y + 1
# tree density - 18
Y[,idx_y] <- (Covariates[,17] - mean(as.vector(Covariates[,17]))) /
sd(as.vector(Covariates[,17]))
idx_y <- idx_y + 1
# No food trees - 19
Y[,idx_y] <- (Covariates[,18] - mean(as.vector(Covariates[,18]))) /
sd(as.vector(Covariates[,18]))
idx_y <- idx_y + 1
# BA FT - 20
Y[,idx_y] <- (Covariates[,19] - mean(as.vector(Covariates[,19]))) /
sd(as.vector(Covariates[,19]))
idx_y <- idx_y + 1
# No stumps - 21
Y[,idx_y] <- (Covariates[,20] - mean(as.vector(Covariates[,20]))) /
sd(as.vector(Covariates[,20]))
idx_y <- idx_y + 1
# shape index - 22

```

```

Y[,idx_y]      <-      (Covariates[,21]      -      mean(as.vector(Covariates[,21])))      /
sd(as.vector(Covariates[,21]))
idx_y <- idx_y + 1

#fill Z
# 1's - 1
Z[,1] <- matrix(1,nrow=nrow(Covariates),ncol=1)
# index
idx_z <- 2
# fragment size - 2
Z[,idx_z]      <-      (Covariates[,1]      -      mean(as.vector(Covariates[,1])))      /
sd(as.vector(Covariates[,1]))
idx_z <- idx_z + 1
# plants - 3
Z[,idx_z]      <-      (Covariates[,2]      -      mean(as.vector(Covariates[,2])))      /
sd(as.vector(Covariates[,2]))
idx_z <- idx_z + 1
# canopy height - 4
Z[,idx_z]      <-      (Covariates[,3]      -      mean(as.vector(Covariates[,3])))      /
sd(as.vector(Covariates[,3]))
idx_z <- idx_z + 1
# canopy cover - 5
Z[,idx_z]      <-      (Covariates[,4]      -      mean(as.vector(Covariates[,4])))      /
sd(as.vector(Covariates[,4]))
idx_z <- idx_z + 1
# % cover 500m - 6
Z[,idx_z]      <-      (Covariates[,5]      -      mean(as.vector(Covariates[,5])))      /
sd(as.vector(Covariates[,5]))
idx_z <- idx_z + 1
# patch density 500m - 7
Z[,idx_z]      <-      (Covariates[,6]      -      mean(as.vector(Covariates[,6])))      /
sd(as.vector(Covariates[,6]))
idx_z <- idx_z + 1
# patch density 1000m - 8

```

```

Z[,idx_z]      <-      (Covariates[,7]      -      mean(as.vector(Covariates[,7])))      /
sd(as.vector(Covariates[,7]))
idx_z <- idx_z + 1
# % cover 1000m - 9
Z[,idx_z]      <-      (Covariates[,8]      -      mean(as.vector(Covariates[,8])))      /
sd(as.vector(Covariates[,8]))
idx_z <- idx_z + 1
# patch density 2500m - 10
Z[,idx_z]      <-      (Covariates[,9]      -      mean(as.vector(Covariates[,9])))      /
sd(as.vector(Covariates[,9]))
idx_z <- idx_z + 1
# % cover 2500m - 11
Z[,idx_z]      <-      (Covariates[,10]     -      mean(as.vector(Covariates[,10])))      /
sd(as.vector(Covariates[,10]))
idx_z <- idx_z + 1
# matrix - 12
Z[,idx_z] <- ifelse(Covariates[,11]==1,0,1)
idx_z <- idx_z + 1
# hedgerows - 13
Z[,idx_z] <- ifelse(Covariates[,12]==1,0,1)
idx_z <- idx_z + 1
# basal area - 14
Z[,idx_z]      <-      (Covariates[,13]      -      mean(as.vector(Covariates[,13])))      /
sd(as.vector(Covariates[,13]))
idx_z <- idx_z + 1
# fruit - 15
Z[,idx_z]      <-      (Covariates[,14]      -      mean(as.vector(Covariates[,14])))      /
sd(as.vector(Covariates[,14]))
idx_z <- idx_z + 1
# flowers - 16
Z[,idx_z]      <-      (Covariates[,15]      -      mean(as.vector(Covariates[,15])))      /
sd(as.vector(Covariates[,15]))
idx_z <- idx_z + 1
# young leaves - 17

```



```

Z[,idx_z]      <-      (Covariates[,16]      -      mean(as.vector(Covariates[,16])))      /
sd(as.vector(Covariates[,16]))
idx_z <- idx_z + 1
# tree density - 18
Z[,idx_z]      <-      (Covariates[,17]      -      mean(as.vector(Covariates[,17])))      /
sd(as.vector(Covariates[,17]))
idx_z <- idx_z + 1
# No food trees - 19
Z[,idx_z]      <-      (Covariates[,18]      -      mean(as.vector(Covariates[,18])))      /
sd(as.vector(Covariates[,18]))
idx_z <- idx_z + 1
# BA FT - 20
Z[,idx_z]      <-      (Covariates[,19]      -      mean(as.vector(Covariates[,19])))      /
sd(as.vector(Covariates[,19]))
idx_z <- idx_z + 1
# No stumps - 21
Z[,idx_z]      <-      (Covariates[,20]      -      mean(as.vector(Covariates[,20])))      /
sd(as.vector(Covariates[,20]))
idx_z <- idx_z + 1
# shape index - 22
Z[,idx_z]      <-      (Covariates[,21]      -      mean(as.vector(Covariates[,21])))      /
sd(as.vector(Covariates[,21]))
idx_z <- idx_z + 1

#fill XP
# 1's - 1
XP[,1] <- matrix(1,nrow=nrow(Cov_Pred),ncol=1)
# index
idx_x <- 2
# fragment size - 2
XP[,idx_x]      <-      (Cov_Pred[,1]      -      mean(as.vector(Cov_Pred[,1])))      /
sd(as.vector(Cov_Pred[,1]))
idx_x <- idx_x + 1
# plants - 3

```

```

XP[,idx_x]      <-      (Cov_Pred[,2]      -      mean(as.vector(Cov_Pred[,2])))      /
sd(as.vector(Cov_Pred[,2]))
idx_x <- idx_x + 1
# canopy height - 4
XP[,idx_x]      <-      (Cov_Pred[,3]      -      mean(as.vector(Cov_Pred[,3])))      /
sd(as.vector(Cov_Pred[,3]))
idx_x <- idx_x + 1
# canopy cover - 5
XP[,idx_x]      <-      (Cov_Pred[,4]      -      mean(as.vector(Cov_Pred[,4])))      /
sd(as.vector(Cov_Pred[,4]))
idx_x <- idx_x + 1
# % cover 500m - 6
XP[,idx_x]      <-      (Cov_Pred[,5]      -      mean(as.vector(Cov_Pred[,5])))      /
sd(as.vector(Cov_Pred[,5]))
idx_x <- idx_x + 1
# patch density 500m - 7
XP[,idx_x]      <-      (Cov_Pred[,6]      -      mean(as.vector(Cov_Pred[,6])))      /
sd(as.vector(Cov_Pred[,6]))
idx_x <- idx_x + 1
# patch density 1000m - 8
XP[,idx_x]      <-      (Cov_Pred[,7]      -      mean(as.vector(Cov_Pred[,7])))      /
sd(as.vector(Cov_Pred[,7]))
idx_x <- idx_x + 1
# % cover 1000m - 9
XP[,idx_x]      <-      (Cov_Pred[,8]      -      mean(as.vector(Cov_Pred[,8])))      /
sd(as.vector(Cov_Pred[,8]))
idx_x <- idx_x + 1
# patch density 2500m - 10
XP[,idx_x]      <-      (Cov_Pred[,9]      -      mean(as.vector(Cov_Pred[,9])))      /
sd(as.vector(Cov_Pred[,9]))
idx_x <- idx_x + 1
# % cover 2500m - 11
XP[,idx_x]      <-      (Cov_Pred[,10]     -      mean(as.vector(Cov_Pred[,10])))      /
sd(as.vector(Cov_Pred[,10]))
idx_x <- idx_x + 1

```

```

# matrix - 12
XP[,idx_x] <- ifelse(Cov_Pred[,11]==1,0,1)
idx_x <- idx_x + 1
# hedgerows - 13
XP[,idx_x] <- ifelse(Cov_Pred[,12]==1,0,1)
idx_x <- idx_x + 1
# basal area - 14
XP[,idx_x] <- (Cov_Pred[,13] - mean(as.vector(Cov_Pred[,13]))) /
sd(as.vector(Cov_Pred[,13]))
idx_x <- idx_x + 1
# fruit - 15
XP[,idx_x] <- (Cov_Pred[,14] - mean(as.vector(Cov_Pred[,14]))) /
sd(as.vector(Cov_Pred[,14]))
idx_x <- idx_x + 1
# flowers - 16
XP[,idx_x] <- (Cov_Pred[,15] - mean(as.vector(Cov_Pred[,15]))) /
sd(as.vector(Cov_Pred[,15]))
idx_x <- idx_x + 1
# young leaves - 17
XP[,idx_x] <- (Cov_Pred[,16] - mean(as.vector(Cov_Pred[,16]))) /
sd(as.vector(Cov_Pred[,16]))
idx_x <- idx_x + 1
# tree density - 18
XP[,idx_x] <- (Cov_Pred[,17] - mean(as.vector(Cov_Pred[,17]))) /
sd(as.vector(Cov_Pred[,17]))
idx_x <- idx_x + 1
# No food trees - 19
XP[,idx_x] <- (Cov_Pred[,18] - mean(as.vector(Cov_Pred[,18]))) /
sd(as.vector(Cov_Pred[,18]))
idx_x <- idx_x + 1
# BA FT - 20
XP[,idx_x] <- (Cov_Pred[,19] - mean(as.vector(Cov_Pred[,19]))) /
sd(as.vector(Cov_Pred[,19]))
idx_x <- idx_x + 1
# No stumps - 21

```

```

XP[,idx_x]      <-      (Cov_Pred[,20]      -      mean(as.vector(Cov_Pred[,20])))      /
sd(as.vector(Cov_Pred[,20]))
idx_x <- idx_x + 1
# shape index - 22
XP[,idx_x]      <-      (Cov_Pred[,21]      -      mean(as.vector(Cov_Pred[,21])))      /
sd(as.vector(Cov_Pred[,21]))
idx_x <- idx_x + 1

#fill YP
# 1's - 1
YP[,1] <- matrix(1,nrow=nrow(Cov_Pred),ncol=1)
# index
idx_y <- 2
# fragment size - 2
YP[,idx_y]      <-      (Cov_Pred[,1]      -      mean(as.vector(Cov_Pred[,1])))      /
sd(as.vector(Cov_Pred[,1]))
idx_y <- idx_y + 1
# plants - 3
YP[,idx_y]      <-      (Cov_Pred[,2]      -      mean(as.vector(Cov_Pred[,2])))      /
sd(as.vector(Cov_Pred[,2]))
idx_y <- idx_y + 1
# canopy height - 4
YP[,idx_y]      <-      (Cov_Pred[,3]      -      mean(as.vector(Cov_Pred[,3])))      /
sd(as.vector(Cov_Pred[,3]))
idx_y <- idx_y + 1
# canopy cover - 5
YP[,idx_y]      <-      (Cov_Pred[,4]      -      mean(as.vector(Cov_Pred[,4])))      /
sd(as.vector(Cov_Pred[,4]))
idx_y <- idx_y + 1
# % cover 500m - 6
YP[,idx_y]      <-      (Cov_Pred[,5]      -      mean(as.vector(Cov_Pred[,5])))      /
sd(as.vector(Cov_Pred[,5]))
idx_y <- idx_y + 1
# patch density 500m - 7

```

```

YP[,idx_y]      <-      (Cov_Pred[,6]      -      mean(as.vector(Cov_Pred[,6])))      /
sd(as.vector(Cov_Pred[,6]))
idx_y <- idx_y + 1
# patch density 1000m - 8
YP[,idx_y]      <-      (Cov_Pred[,7]      -      mean(as.vector(Cov_Pred[,7])))      /
sd(as.vector(Cov_Pred[,7]))
idx_y <- idx_y + 1
# % cover 1000m - 9
YP[,idx_y]      <-      (Cov_Pred[,8]      -      mean(as.vector(Cov_Pred[,8])))      /
sd(as.vector(Cov_Pred[,8]))
idx_y <- idx_y + 1
# patch density 2500m - 10
YP[,idx_y] <- (Cov_Pred[,9] - mean(as.vector(Cov_Pred[,9]))) / sd(as.vector(Cov_Pred[,9]))
idx_y <- idx_y + 1
# % cover 2500m - 11
YP[,idx_y]      <-      (Cov_Pred[,10]     -      mean(as.vector(Cov_Pred[,10])))      /
sd(as.vector(Cov_Pred[,10]))
idx_y <- idx_y + 1
# matrix - 12
YP[,idx_y] <- ifelse(Cov_Pred[,11]==1,0,1)
idx_y <- idx_y + 1
# hedgerows - 13
Yp[,idx_y] <- ifelse(Cov_Pred[,12]==1,0,1)
idx_y <- idx_y + 1
# basal area - 14
YP[,idx_y]      <-      (Cov_Pred[,13]     -      mean(as.vector(Cov_Pred[,13])))      /
sd(as.vector(Cov_Pred[,13]))
idx_y <- idx_y + 1
# fruit - 15
YP[,idx_y]      <-      (Cov_Pred[,14]     -      mean(as.vector(Cov_Pred[,14])))      /
sd(as.vector(Cov_Pred[,14]))
idx_y <- idx_y + 1
# flowers - 16
YP[,idx_y]      <-      (Cov_Pred[,15]     -      mean(as.vector(Cov_Pred[,15])))      /
sd(as.vector(Cov_Pred[,15]))

```

```

idx_y <- idx_y + 1
# young leaves - 17
YP[,idx_y] <- (Cov_Pred[,16] - mean(as.vector(Cov_Pred[,16]))) /
sd(as.vector(Cov_Pred[,16]))
idx_y <- idx_y + 1
# tree density - 18
YP[,idx_y] <- (Cov_Pred[,17] - mean(as.vector(Cov_Pred[,17]))) /
sd(as.vector(Cov_Pred[,17]))
idx_y <- idx_y + 1
# No food trees - 19
YP[,idx_y] <- (Cov_Pred[,18] - mean(as.vector(Cov_Pred[,18]))) /
sd(as.vector(Cov_Pred[,18]))
idx_y <- idx_y + 1
# BA FT - 20
YP[,idx_y] <- (Cov_Pred[,19] - mean(as.vector(Cov_Pred[,19]))) /
sd(as.vector(Cov_Pred[,19]))
idx_y <- idx_y + 1
# No stumps - 21
YP[,idx_y] <- (Cov_Pred[,20] - mean(as.vector(Cov_Pred[,20]))) /
sd(as.vector(Cov_Pred[,20]))
idx_y <- idx_y + 1
# shape index - 22
YP[,idx_y] <- (Cov_Pred[,21] - mean(as.vector(Cov_Pred[,21]))) /
sd(as.vector(Cov_Pred[,21]))
idx_y <- idx_y + 1

X_temp <- X[,c(1,2,4,9,12,13,15,19)]
Y_temp <- Y[,c(1,2,4,9,12,13,15,19)]
Z_temp <- Z[,c(1,2,4,9,12,13,15,19)]
XP_temp <- XP[,c(1,2,4,9,12,13,15,19)]
YP_temp <- YP[,c(1,2,4,9,12,13,15,19)]

data1 <-
list(NGROUPS=as.matrix(NGROUPS),COMP=as.matrix(COMP),GSIZE=as.matrix(GSIZE)
,SITE=as.matrix(SITE),NSURVEYS=as.matrix(NSURVEYS),X=X_temp,Y=Y_temp,Z=Z_te

```

```
mp,CSITES=dim(X_temp)[1],CGROUPS=dim(GSIZE)[1],Nx=dim(X_temp)[2],Ny=dim(Y_temp)[2],Nz=dim(Z_temp)[2],zeros=matrix(0,nrow=dim(GSIZE)[1],ncol=1),CSITES=dim(XP_temp)[1],XP=XP_temp,YP=YP_temp)
```

```
#combine data
data <- data1
source("./code/functions.r")
Jags.Fit <- get.jags.sel.pred(data)
save(Jags.Pred,file="Jags_Pred.RData")
```

## Functions R Code

```
get.jags <- function(Data)
{
  get_G <- function(NGroups)
  {
    Max <- apply(NGroups,MARGIN=1,FUN=function(X){max(X,na.rm=T)})

    G <- matrix(ceiling(runif(nrow(NGroups),Max,10)),nrow=nrow(NGroups),ncol=1)

    return(G)
  }

  #get initial values
  inits1 <- list(alpha=runif(Data$Nx,-5,5),beta=runif(Data$Ny,-1,1),gamma=matrix(runif(Data$Nz * 2,-5,5),nrow=2,ncol=Data$Nz),gamma_size=runif(2,-5,5),c=runif(1,-5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))
  inits2 <- list(alpha=runif(Data$Nx,-5,5),beta=runif(Data$Ny,-1,1),gamma=matrix(runif(Data$Nz * 2,-5,5),nrow=2,ncol=Data$Nz),gamma_size=runif(2,-5,5),c=runif(1,-5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))
  inits3 <- list(alpha=runif(Data$Nx,-5,5),beta=runif(Data$Ny,-1,1),gamma=matrix(runif(Data$Nz * 2,-5,5),nrow=2,ncol=Data$Nz),gamma_size=runif(2,-5,5),c=runif(1,-5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))

  cl <- makeCluster(3)
```

```

fit                                                                                                     <-
run.jags(model="E:/Projects/colombian_primates/models/code/jags_model_primates.txt",m
onitor=c("alpha","beta","gamma","gamma_size","p"),data=Data,n.chains=3,init
nits2,init3),burnin=20000,adapt=1000,sample=20000,jags="C:/Program
Files/JAGS/JAGS-3.4.0/x64/bin/jags-terminal.exe",method="rjparallel",cl=cl)

stopCluster(cl)

return(fit)
}

get.jags.sel <- function(Data)
{
  get_G <- function(NGroups)
  {
    Max <- apply(NGroups,MARGIN=1,FUN=function(X){max(X,na.rm=T)})

    G                                                                                                     <-
matrix(ceiling(runif(nrow(NGroups),Max,10)),nrow=nrow(NGroups),ncol=1)

    return(G)
  }

  #get initial values
  inits1 <- list(alphaT=runif(Data$Nx,-5,5),ingps=c(NA,round(runif(Data$Nx, -
1,0,1))),pngps=runif(1,0,1),taua=runif(1,0,5),betaT=runif(Data$Ny, -
1,1),isgps=c(NA,round(runif(Data$Ny, -
1,0,1))),psgps=runif(1,0,1),taub=runif(1,0,5),gammaT=matrix(runif(Data$Nz * 2,-
5,5),nrow=2,ncol=Data$Nz),gamma_sizeT=runif(2,-
5,5),icomp=cbind(c(NA,NA),matrix(round(runif(Data$Nz *
2,0,1)),nrow=2,ncol=Data$Nz)),pcomp=runif(2,0,1),taug=runif(1,0,5),c=runif(1,-
5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))

  inits2 <- list(alphaT=runif(Data$Nx,-5,5),ingps=c(NA,round(runif(Data$Nx, -
1,0,1))),pngps=runif(1,0,1),taua=runif(1,0,5),betaT=runif(Data$Ny, -

```



```

1,1),isgps=c(NA,round(runif(Data$Ny
1,0,1))),psgps=runif(1,0,1),taub=runif(1,0,5),gammaT=matrix(runif(Data$Nz      *      2,-
5,5),nrow=2,ncol=Data$Nz),gamma_sizeT=runif(2,-
5,5),icomp=cbind(c(NA,NA),matrix(round(runif(Data$Nz      *
2,0,1))),nrow=2,ncol=Data$Nz)),pcomp=runif(2,0,1),taug=runif(1,0,5),c=runif(1,-
5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))

  inits3    <-    list(alphaT=runif(Data$Nx,-5,5),ingps=c(NA,round(runif(Data$Nx    -
1,0,1))),pngps=runif(1,0,1),taua=runif(1,0,5),betaT=runif(Data$Ny,-
1,1),isgps=c(NA,round(runif(Data$Ny      -
1,0,1))),psgps=runif(1,0,1),taub=runif(1,0,5),gammaT=matrix(runif(Data$Nz      *      2,-
5,5),nrow=2,ncol=Data$Nz),gamma_sizeT=runif(2,-
5,5),icomp=cbind(c(NA,NA),matrix(round(runif(Data$Nz      *
2,0,1))),nrow=2,ncol=Data$Nz)),pcomp=runif(2,0,1),taug=runif(1,0,5),c=runif(1,-
5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))

  cl <- makeCluster(3)

  fit                                     <-
run.jags(model="E:/Projects/colombian_primates/models/code/jags_model_primates_sele
ction.txt",monitor=c("alpha","beta","gamma","gamma_size","ingps","isgps","icomp","p"),dat
a=Data,n.chains=3,inits=list(inits1,inits2,inits3),burnin=20000,adapt=1000,sample=20000,j
ags="C:/Program                               Files/JAGS/JAGS-3.4.0/x64/bin/jags-
terminal.exe",method="rjparallel",cl=cl)

  stopCluster(cl)

  return(fit)
}

get.jags.sel.pred <- function(Data)
{
  get_G <- function(NGroups)
  {
    Max <- apply(NGroups,MARGIN=1,FUN=function(X){max(X,na.rm=T)})

```

```

      G                                                                 <-
matrix(ceiling(runif(nrow(NGroups),Max,10)),nrow=nrow(NGroups),ncol=1)

      return(G)
}

#get initial values
      inits1    <-    list(alphaT=runif(Data$Nx,-5,5),ingps=c(NA,round(runif(Data$Nx
1,0,1))),pngps=runif(1,0,1),taua=runif(1,0,5),betaT=runif(Data$Ny,-
1,1),isgps=c(NA,round(runif(Data$Ny
1,0,1))),psgps=runif(1,0,1),taub=runif(1,0,5),gammaT=matrix(runif(Data$Nz      *      2,-
5,5),nrow=2,ncol=Data$Nz),gamma_sizeT=runif(2,-
5,5),icomp=cbind(c(NA,NA),matrix(round(runif(Data$Nz      *
2,0,1))),nrow=2,ncol=Data$Nz)),pcomp=runif(2,0,1),taug=runif(1,0,5),c=runif(1,-
5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))
      inits2    <-    list(alphaT=runif(Data$Nx,-5,5),ingps=c(NA,round(runif(Data$Nx
1,0,1))),pngps=runif(1,0,1),taua=runif(1,0,5),betaT=runif(Data$Ny,-
1,1),isgps=c(NA,round(runif(Data$Ny
1,0,1))),psgps=runif(1,0,1),taub=runif(1,0,5),gammaT=matrix(runif(Data$Nz      *      2,-
5,5),nrow=2,ncol=Data$Nz),gamma_sizeT=runif(2,-
5,5),icomp=cbind(c(NA,NA),matrix(round(runif(Data$Nz      *
2,0,1))),nrow=2,ncol=Data$Nz)),pcomp=runif(2,0,1),taug=runif(1,0,5),c=runif(1,-
5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))
      inits3    <-    list(alphaT=runif(Data$Nx,-5,5),ingps=c(NA,round(runif(Data$Nx
1,0,1))),pngps=runif(1,0,1),taua=runif(1,0,5),betaT=runif(Data$Ny,-
1,1),isgps=c(NA,round(runif(Data$Ny
1,0,1))),psgps=runif(1,0,1),taub=runif(1,0,5),gammaT=matrix(runif(Data$Nz      *      2,-
5,5),nrow=2,ncol=Data$Nz),gamma_sizeT=runif(2,-
5,5),icomp=cbind(c(NA,NA),matrix(round(runif(Data$Nz      *
2,0,1))),nrow=2,ncol=Data$Nz)),pcomp=runif(2,0,1),taug=runif(1,0,5),c=runif(1,-
5,5),p=runif(1,0,1),G=get_G(Data$NGROUPS))

      cl <- makeCluster(3)

```

```

fit
run.jags(model="E:/Projects/colombian_primates/models/prediction_code/jags_model_pri
mates_selection_pred.txt",monitor=c("lambdap","etap","abundp"),data=Data,n.chains=3,ini
ts=list(inits1,inits2,inits3),burnin=20000,adapt=1000,sample=20000,jags="C:/Program
Files/JAGS/JAGS-3.4.0/x64/bin/jags-terminal.exe",method="rjparallel",cl=cl)

stopCluster(cl)

return(fit)
}

```